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AN ANALYSIS OF FOUR YEARS CAPTURES OF INSECTS IN A LIGHT TRAP. PART II.¹ THE EFFECT OF WEATHER CONDITIONS ON INSECT ACTIVITY; AND THE ESTIMATION AND FORECASTING OF CHANGES IN THE INSECT POPULATION

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(Read 7th February, 1940.)

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INTRODUCTORY AND OUTLINE OF ARGUMENT.

A LIGHT trap, with an electric light of approximately 300 candle-power at a height of about 3 feet 6 inches above the ground, was exposed in one of the fields at Rothamsted Experimental Station, Harpenden, about 25 miles north of London, on a total of 1407 nights between the 1st March 1933 and the 28th February 1937. The catch each night was counted and sorted into orders, and some of the orders again sorted to families and species. The total catches in the four successive years were 109,344; 103,362; 399,006 and 242,822 insects respectively. The number caught per night varied from zero on many nights in the winter months to a maximum of approximately 73,000 on one night at the end of June 1935. There were, however, only 13 occasions when the catch was over 10,000 insects and these were all in 1935 and 1936.

A full account of the trap has already been published (Williams 1935), and in the first half of this present paper (Williams 1939) the results have been discussed in their bearings on the distribution of the catch among the different orders of insects, the sex proportions, phenology and the time of flight during the night.

The present section is an attempt to analyse the results in so far as they throw light on the problem of the influence of weather conditions on the catches; and hence, if one assumes the catches to be a representative sample, on the activity and on the basic population of the insects.

As this analysis is rather long and complicated, and as it contains references to methods that were found unsuccessful as well as to those that were successful, it has been thought desirable to start with an outline of the method and results in order that the threads can be more easily held together later.

The argument developed is as follows: The number of insects caught in the trap on any one night is mainly determined by two factors; (1) the activity of the insects, and (2) the total population available for sampling.

The activity varies rapidly from hour to hour and from night to night and is determined largely by the weather conditions of the moment, and (in this locality) particularly by temperature and wind and to a less extent by humidity and other factors.

The population changes happen more slowly and are determined more by the weather conditions some time previous than by those at the moment; except perhaps in the case of the sudden emergence of a large number of insects from the pupal stage when the weather becomes warm after a cold spell.

Thus, if one considers the difference in catch between two successive nights,

the effect will be largely due to activity; whilst the difference in catch between two similar nights in different months will be largely due to population. The difference in average catch between June of one year and June of another will be still more dependent on population differences.

By the statistical method of "partial regressions" and by using as data the difference between successive days, values have been obtained which it is believed show very closely the "activity" effect on the catch due to unit changes in the maximum temperature of the previous day, the minimum temperature of the night, the wind force during the night, etc. These have been expressed as percentage changes in catch. Thus it will be shown that 1° F. increase in minimum temperature of the night adds on an average 18% to the catch; 1° F. increase in maximum temperature adds 5% to the catch, and one group increase in wind (see later for explanation) reduces the catch by 28%.

These values can be used to correct the mean catch in any one month for the departures of that month's weather conditions from the normal. A new figure is thus obtained for what the mean catch for that month would have been if weather conditions had all been normal. If these "mean catch values under normal conditions" are calculated for the same month in a series of years the differences between them (assuming that errors are as likely in one direction as another) are measures of the population differences between the months.

In this way a measure of the percentage or logarithmic departure of the population from the normal has been obtained from the trap data over a series of 48 months. The method of partial regressions can now be applied to these figures to show to what extent they can be accounted for by changes in the weather conditions in the preceding months. The factors taken for this were minimum temperature and rainfall in the three months previous; and two series of regressions have been obtained: one for summer (May to October) and one for winter (November to April). The figures show that in winter, temperature is the most important factor and rainfall can be practically neglected; while in summer rainfall is the most important factor and temperature changes can be neglected.

From the regressions thus obtained a forecast of the probable population changes can be made from a knowledge of the weather conditions in the three months previous to the forecast, without using the trap figures.

When these estimations are made and compared with the population changes calculated from the trap catch it is found that 50-60% of the variance of the latter can be accounted for; and undoubtedly a higher figure could be obtained if data were available to calculate separate regression values for spring, summer, autumn and winter.

The method has so far only been applied to the total insect catch (that is to say, to the sample thus obtained of the total positively phototropic night population). New data are being collected and the analysis continued to see to what extent the methods can be applied to single species; and how the difficulties, arising from the rapid rise and fall of population during a brood, can be overcome. An attempt has been made in this paper to explain graphically some of the mathematical processes used, and to develop them from simple examples to more complicated ones, so that the main principles of both method and results can be understood by any entomologist with some knowledge of mathematics. The work will lose half its value if the mathematical side is only understood by statisticians with no knowledge of the idiosyncrasies of insects, and the entomological side only by entomologists who fail to understand that mathematics is only a condensed form of reasoning.

METEOROLOGICAL RECORDS AVAILABLE.

Rothamsted Experimental Station ranks as a First-Class Meteorological Station and the majority of the records are taken within 240 yards of the trap itself.

Records are available on continuously recording instruments of barometric pressure, air screen temperature, rainfall, wind (direction and force), total radiation, bright sunshine and (for most of the years) relative humidity. Records are taken once or twice a day of many other factors, including air screen temperature, soil temperature at various depths, and wet- and dry-bulb temperatures. Maximum and minimum temperatures are recorded daily in the screen, and also the minimum on the ground (grass minimum) and the maximum of the black bulb in the sun. Notes are also taken each day of the prevalence of dew, fog, snow, frost, etc. etc.

In addition to the above it was found necessary for the present investigation to add instruments for measuring the duration of bright moonlight (see Williams and Emery 1935) and the duration of night cloud. The instrument for the latter was adapted from one already in use at Greenwich Observatory (see Anon. 1931 and Williams 1936b).

There was, therefore, available for comparison with the trap captures an excellent series of measurements of the physical environment; and, as many of the records have been taken for over fifty years, good average values were available as a measure of normal conditions.

All temperatures are given as ° F. unless otherwise stated.

Normal climatic conditions at Rothamsted.

Table 1 shows the average values of some of the principal climatic factors for the station.

TABLE 1.

Mean weather conditions at Rothamsted over 39-79 years and figures showing how the conditions in the four trap years differed from the long-period means.

	Temperature						Daily range	Sunshine		Rain		Rainy days
	Max.		Min.		Mean			Hrs. per day		In. per month		
	50 yrs.	4 yrs.	50 yrs.	4 yrs.	50 yrs.	4 yrs.		39 yrs.	4 yrs.	79 yrs.	4 yrs.	
March	48-6	1.7	34.1	2.0	41.1	1.9	14.1 - 0.3	3.74	0.65	1.992	0.286	14 ± 0
April	53-6	1.4	37.3	1.1	45.5	0.1	16.4 - 2.4	5.22	0.82	1.985	0.228	13 - 0.5
May	60.9	0.6	44.1	0.9	52.5	0.7	16.8 + 0.4	6.60	0.63	2.152	1.021	13 - 3
June	66.1	0.9	48.4	1.9	57.2	1.5	17.7 - 1.0	6.81	0.12	2.243	0.655	12 + 3
July	69.4	2.3	52.0	1.8	60.7	2.0	17.4 + 0.6	6.50	0.94	2.640	0.664	13 - 3
Aug.	68.4	2.4	51.6	0.8	59.9	1.7	16.7 + 1.7	6.05	0.47	2.659	1.625	14 - 5.5
Sept.	63.8	1.3	47.9	2.7	55.8	2.0	15.9 - 1.4	5.10	0.18	2.391	0.715	13 + 1
Oct.	55.6	0.5	42.1	1.0	48.9	0.2	13.5 - 1.5	3.50	0.36	3.059	1.155	17 - 1
Nov.	47.9	1.3	36.6	0.4	42.3	0.5	11.3 - 1.7	2.17	0.46	2.701	0.220	16 - 2
Dec.	43.8	1.0	33.8	0.8	38.8	0.1	10.0 - 1.8	1.41	0.05	2.637	0.089	17 - 0.5
Jan.	42.8	0.4	32.6	1.5	37.7	1.0	10.2 - 1.1	1.68	0.08	2.427	0.304	17 + 1
Feb.	43.8 ± 0		32.5 + 1.0		38.1 + 0.5		11.2 - 1.2	2.46 + 0.14		1.910 + 0.338		14 + 1
Year	—		—		—		—	1561 hrs.		28.72 ins.		173

It will be seen that, during the past 50 years, July has the highest average maximum temperature (69.4° F.) and January the lowest (42.8° F.). July has also the highest minimum (52° F.) and February the lowest (32.5° F.). July and January have respectively the highest and lowest mean temperatures (60.7 and 37.7° F.); the annual range of the mean temperature is therefore only 23° F.

The sunshine has averaged 1561 hours per year (39 years). June has the highest, 6.81 hours per day and December the lowest, 1.41 hours per day.

The rainfall is low and is evenly distributed throughout the year. The average (79 years) is 28.7 inches and no month averages less than 1.9 or over 3.1 inches. The number of rainy days (*i.e.* days with 0.01 inch or over per day) is also very even throughout the year. There is, as is usual in England, no definite wet or dry season.

Weather in the four trap years.

As it is only possible to compare the catch in each of the four trap years with the mean catch during the four years it has been considered necessary that any comparisons made in weather conditions should be with a similar mean.

Table 1 therefore shows how the mean of the four years in which the trap was used differed from the long-range means; and Table 2 shows how each of the four years differed from their own mean.

An examination of Table 1 shows that the 4 years average minimum temperatures were above the 50 years normal in all months except May, and that the maximum temperatures were above the average in January and March and in June to September. Sunshine was only above the average in February and March and in July and August. Rainfall was in general below the average.

An examination of Table 2 shows that the successive years differed as follows from the four year average.

TABLE 2.

Departures of the chief weather factors in the four trap years from the average of these four years.

Temperature	Max.				Min.				Mean				Daily range			
	33	34	35	36	33	34	35	36	33	34	35	36	33	34	35	36
March	+3.3	-2.8	-0.5	-0.1	+0.1	-2.5	±0	+2.2	+1.7	-2.7	-0.2	+1.0	+3.2	-0.3	-0.5	-2.3
April	+3.0	+1.2	-0.5	-3.8	+1.1	+0.2	+0.6	-2.0	+2.0	+0.7	±0	-2.9	+1.9	+1.0	-1.1	-1.8
May	+1.1	+0.8	-2.6	+0.8	+2.0	-0.4	-2.0	+0.2	+1.5	+0.1	-2.3	+0.5	-1.0	+1.1	-0.7	+0.5
June	+1.4	+0.4	-0.8	1.0	-0.6	-0.5	+0.8	+0.4	+0.4	-0.1	-0.1	-0.4	+2.0	+0.9	-1.6	-1.4
July	+1.8	+3.3	+1.1	-6.2	+1.5	-0.5	-0.4	-0.8	+1.7	+1.4	+0.4	-3.4	+0.2	+3.7	+1.4	-5.5
Aug.	+3.7	-2.3	+1.0	-2.3	+1.7	-1.5	±0	-0.2	+2.7	-1.9	+0.5	-1.3	+2.0	-0.8	+1.0	-2.1
Sept.	+2.2	+1.7	-1.6	-2.4	+0.8	-0.8	-1.3	+1.4	+1.5	+0.5	-1.4	-0.5	+1.4	+2.5	-0.3	-3.8
Oct.	+0.3	+1.2	-0.6	-1.0	+1.0	+1.5	-0.8	-1.7	+0.6	+1.4	-0.7	-1.4	-0.7	-0.3	+0.2	+0.7
Nov.	-1.5	-0.2	+1.9	-0.2	+0.6	+0.8	+1.0	-2.3	-0.5	+0.3	+1.4	-1.3	-2.1	-1.0	+0.9	+2.1
Dec.	-6.4	+6.3	-1.9	+2.0	-5.2	+7.3	-1.9	±0	-5.8	+6.8	-2.0	+1.0	-1.2	-1.0	+0.2	+2.0
Jan.	-0.1	-0.5	-0.7	+1.4	-2.0	+1.4	-0.5	+1.1	-1.1	+0.4	-0.6	+1.2	+1.9	-1.9	-0.2	+0.3
Feb.	-1.0	+2.5	-4.1	+2.6	-3.0	+3.0	-3.0	+3.1	-1.9	+1.5	-3.5	+3.9	+1.3	-0.2	-0.8	-0.2

	Sunshine (hrs. per day)				Rainfall (in. per month)				Rainy days			
	33	34	35	36	33	34	35	36	33	34	35	36
March	+1.96	-0.29	-0.06	-1.62	+0.98	+0.63	-1.16	-0.46	+2	+2	-4	0
April	+0.71	-0.37	-0.18	-0.17	-0.89	-0.40	+1.82	-0.53	-5.5	+0.5	+6.5	-0.5
May	-0.54	+0.51	+0.28	-0.26	+0.36	-0.30	+0.62	-0.69	+5	-1	-1	-3
June	+1.33	-0.53	-0.19	-0.60	-1.90	-1.23	-0.08	+3.20	-2	-4	+2	+4
July	+0.50	+1.42	+1.60	-3.54	-0.63	-0.91	-1.06	+2.60	-1	-2	-5	+8
Aug.	+1.32	-0.70	-0.06	-0.67	-0.47	+0.74	+0.47	-0.74	-1.5	+4.5	+0.5	-3.5
Sept.	+1.19	+0.83	+0.08	-2.11	-0.84	-0.46	+1.07	+0.22	-4	-3	+2	+4
Oct.	-0.09	-0.40	+0.48	-0.01	-0.57	-0.02	+0.87	-0.27	-2	-2	+4	-1
Nov.	±0	-0.18	+0.35	-0.17	-1.63	-1.17	+2.09	+0.71	-2	-5	+7	0
Dec.	-0.03	-0.69	+0.17	+0.56	-2.11	+2.28	+0.30	-0.47	-9.5	+8.5	+0.5	+0.5
Jan.	+0.24	-0.09	±0	-0.17	-0.79	-1.90	+1.14	+1.55	+1	-8	+1	+5
Feb.	+0.83	-0.71	+0.19	-0.30	-1.80	+0.41	-0.12	+1.51	-9	+4	0	+6

1933-34. *Spring* (March to May). Maximum, minimum and mean temperatures all above average.

Summer (June to August). Maximum and mean temperatures all above average; minimum above average in July and August. Sunshine average. Rainfall below in all months.

- Autumn* (September to November). Minimum temperatures all above average. Maximum above in September and October. Rainfall all below average.
- Winter* (December to February). Maximum and minimum temperatures and rainfall all below average.
- General Characteristics.* Temperatures above average except in winter, rainfall much below average except in spring.
- 1934-35. *Spring.* Minimum temperatures average or below; rainfall above in March, below in April and May.
- Summer.* Minimum temperatures below average; rainfall below in June and July.
- Autumn.* Mean temperatures average; rainfall below.
- Winter.* Minimum temperatures above average especially in December, which had the highest value in 50 years. Maximum temperatures average or above, sunshine below average. Rain above in December, below in January.
- General Characteristics.* Minimum temperatures above average October to February, below in March and May to September. Sunshine generally below average. Rainfall below until the winter when the long drought ended.
- 1935-36. *Spring.* Maximum temperatures below average; rainfall above in April and May, very cold spell in mid-May.
- Summer.* Maximum and mean temperatures and sunshine above normal in July and August; rainfall below in May and June.
- Autumn.* Temperatures below average in September and October, above in November. Rain and sun above normal.
- Winter.* Temperatures all below average. Sunshine average or above. Rainfall above in December and January.
- General Characteristics.* Temperatures rather below average; rainfall above, and previous drought conditions replaced in some places by floods.
- 1936-37. *Spring.* Temperatures irregular. Sun and rain below average.
- Summer.* Temperatures mostly below average. Sun below, rain very high in June and July; 3.088 inches on 21st June.
- Autumn.* Temperatures and sunshine below average; rainfall somewhat above.
- Winter.* Temperatures above average; rainfall much above in January and February.
- General Characteristics.* Generally cool and rain above average.

The highest maximum temperature recorded during the four years was 89.3 on the 27th July 1933 and the lowest maximum 28.3 on 27th January 1937. The highest screen minimum was 65.3 on 3rd August 1933 and the lowest 13.4 on the 23rd December 1935. The total range of air temperature experienced was therefore 75.9° F. (42.2° C.).

The lowest grass minimum was 9.6° F. on the 12th February 1936.

NOTES ON THE STATISTICAL ANALYSIS OF THE RESULTS.

Sources of error.

Efficiency of the trap.

The trap, like all others, is by no means perfect. Some insects may fly round and fail to enter. More rarely some may escape after having entered.

Inefficiencies of this kind, provided that they are constant, should not affect the analysis of the results. The more serious errors are those which alter from time to time. For example, the intensity of the light produced varies approximately as the cube of the voltage. In the first year of use the trap was at the end of a field line over a quarter of a mile long on a 100-volts transformer circuit which was at times much overloaded; as a result the voltage was usually between 85 and 90 instead of 100. This difficulty was overcome by the use of "barretter" stabilising valves (see Williams 1935 : 526). At the end of the first year the current was changed to a main circuit at 240 volts and variations were so much reduced that the barretters were unnecessary.

The candle-power of a lamp also decreases as the lamp is used and is usually 10–15% less after the lamp has been in use for 1000 hours. This deterioration is more rapid if the voltage of the circuit is higher than the standard for the lamp and much slower if the voltage is lower. To reduce the error from this source as far as possible a lamp of the same voltage as the circuit was used, but a resistance of about 700 ohms was placed in parallel with the lamp so that the current going through the lamp was reduced. This lowered its candle-power but greatly increased its length of life at that candle-power.

Any likelihood of insects entering the trap and then escaping can only be reduced by keeping the killing-bottles in good condition. This has been done by renewing them whenever there was any sign of failure.

When using the trap to find the time of flight at night of various insects,

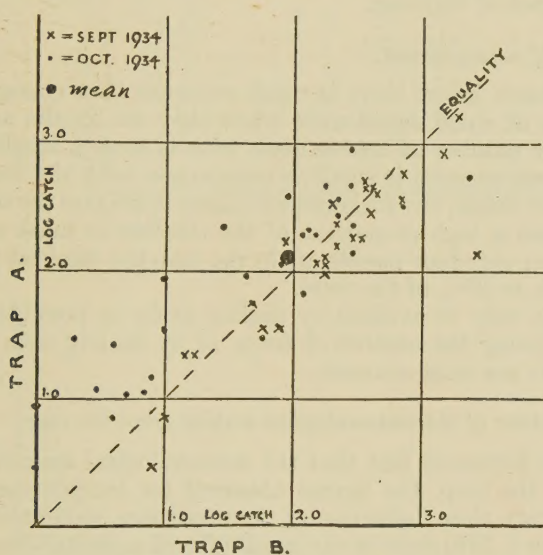


FIG. 1.—Scatter diagram showing relation between simultaneous catches in two light traps during September and October 1934. All insects.

any delay in the insect entering the trap or being killed when it enters may cause all the results to be too late. The trap was under close observation from this point of view on many occasions and it was found that there was seldom a delay of more than three or four minutes between the entry of an insect into the trap and its falling into the killing-bottle. As the minimum length of any period was 50 minutes this delay is of no significance.

Error from using a single trap as sample.

There is no doubt that more reliable results could be obtained by the use of several traps working simultaneously, and if the present investigation is to be continued this change would be recommended. On several occasions, however, a second trap has been in use at the same time as the standard trap. In September and October 1934 the two traps were working about 250 yards apart with almost identical conditions of illumination and outlook.

Fig. 1 shows the relation of the total catches to each other on each night

that the traps were working. The mean log. catch was 2.11 for trap A (the standard trap) and 1.91 for trap B (the additional trap) over the two months. The correlations for all insects was 0.86 for September and 0.92 for October.

In September only the correlation was 0.85 for TIPULIDAE; 0.97 for JASSIDAE, and 0.80 for NOCTUIDAE. Thus it will be seen that there is a very close relation between the two.

A statistical examination of the departures of each day's log. catch from the monthly mean in the two traps during the two months showed the mean square of the difference to be 0.0981. The mean square of the sampling error of a single trap is therefore 0.0491, and the actual sampling error is the square root of this or 0.222. By the method of differences between successive days the mean square of the sampling error is 0.0686. These figures will be used later in the analysis of variance.

Error from unit of measurement.

As will be shown below there is much evidence that changes in numbers in the catch are of equal significance when they are in the same geometric ratio. When the number of insects dealt with is large a single insect, which is the unit of measurement, is small in comparison with the total; but when dealing with a rare insect, or with times when insects are rare the unit of measurement may be such a high proportion of the total as to mask small changes; for example, when only four insects are in the trap the smallest possible reduction is one insect, or 25% of the total.

This error can only be avoided by dealing as far as possible with common insects, by increasing the number of traps, or by dealing with periods of the year when insects are most common.

Error due to distance of the meteorological station from the trap.

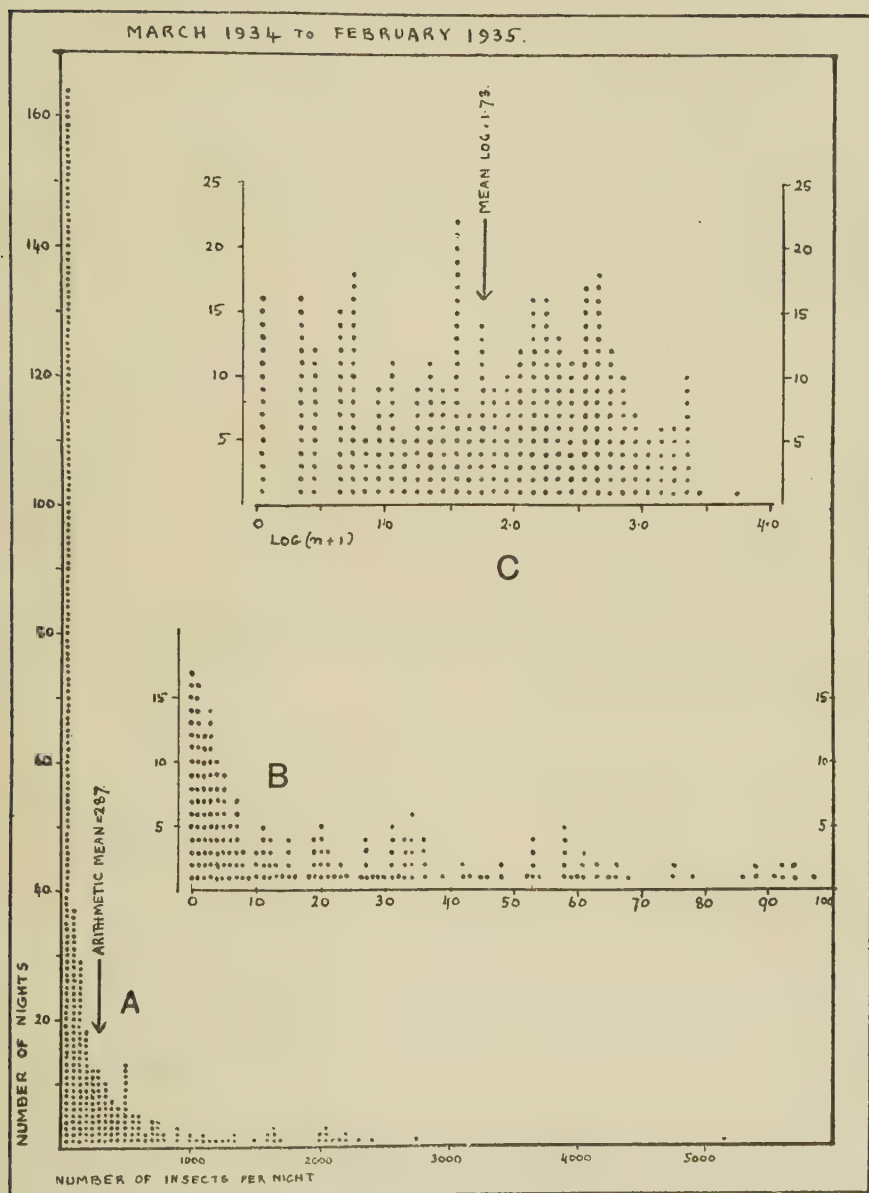
Owing to the fortunate fact that the meteorological station is only about 250 yards from the trap, the figures obtained for temperature and rainfall, etc., must be a very close indication of the conditions round the trap itself.

With wind (see p. 278) there is the possibility of a greater error, as the wind records are taken above the roof of the laboratories about 320 yards away to the east, at a height of about 70 feet from the ground, and so in a considerably more exposed position.

The use of geometric means in analysis.

When the catches in the trap night by night over a period of a year are examined it is found that they consist of a large number of small catches and a small number of large catches. Fig. 2, A shows the frequency distribution of the catches over a complete year from March 1934 to February 1935, arranged in groups of 0-49, 50-99, 100-149, etc. It will be seen that there were 164 nights with fewer than 50 insects, 37 nights with 50-99 insects, etc., and only one night with over 5000 insects. Fig. 2, B shows all the values below 100 arranged in units, from which it will be seen that the peak of the curve is at the zero value.

When the arithmetic mean catch per night (which in this year is 287 insects) is placed on the diagram it will be seen that there are a large number of nights below the mean with small negative departures and a small number of nights above the mean with large positive departures. There are, in fact, 265 nights below and only 95 nights above the arithmetic mean.



2

FIG. 2.—Frequency distribution of catches of all insects during 1934–35 :—
 A = all catches expressed as numbers in groups of 50.
 B = all catches up to 100 per night.
 C = all catches expressed as log. ($n + 1$).

In some of the other years the differences were even greater; for example in 1935-36 there were 181 nights with fewer than 50 insects, and 16 nights with over 5000 per night. Their distribution was 310 below the arithmetic mean (1102) and only 51 above.

It is of course impossible to use the normal formula relating to standard deviation, probable error, correlation and regression for figures showing a strongly asymmetrical distribution of this type.

It was, however, found that a better distribution could be obtained by considering the geometrical ratio between catches, rather than their arithmetic difference, and by using geometric means instead of arithmetic means. A fuller account of the application of the principle has been already published (Williams 1937).

The simplest method of obtaining such results is to deal with the logarithm of the catch number instead of the actual number itself. A difficulty arises, however, from the fact that not infrequently a zero catch is obtained. The log of zero is "minus infinity" and the geometric mean of any series containing zero is itself zero. To overcome this difficulty it has been found practicable to add unity to each of the catches before taking the log: *i.e.* using $\log(n+1)$ instead of $\log n$, where n represents the catch. These values can be summed or averaged for comparison, but should it be desired at any time to convert back to numbers (to find the geometric mean value) then unity must be subtracted from the anti-log.

If this process is used for the plotting of the distribution of the catches in each night of 1934-35 the result is as shown in fig. 2, C where the values of $\log(n+1)$ are divided into groups differing by 0.1. The first column on the left represents the 16 nights with no catch (as $\log(0+1)=0$); the next column represents the 16 nights on which one insect only was caught each night (as $\log(1+1)=0.30$), etc. The mean log value is 1.73 as indicated in the diagram by the vertical arrow.

It will be seen that distribution of the nights is much more normal and evenly placed about the mean. There are in fact 171 values below the mean and 190 above, and the extent of distribution on either side of the mean is almost identical. On a distribution of this type it is possible to use the normal formulae for correlation, etc.

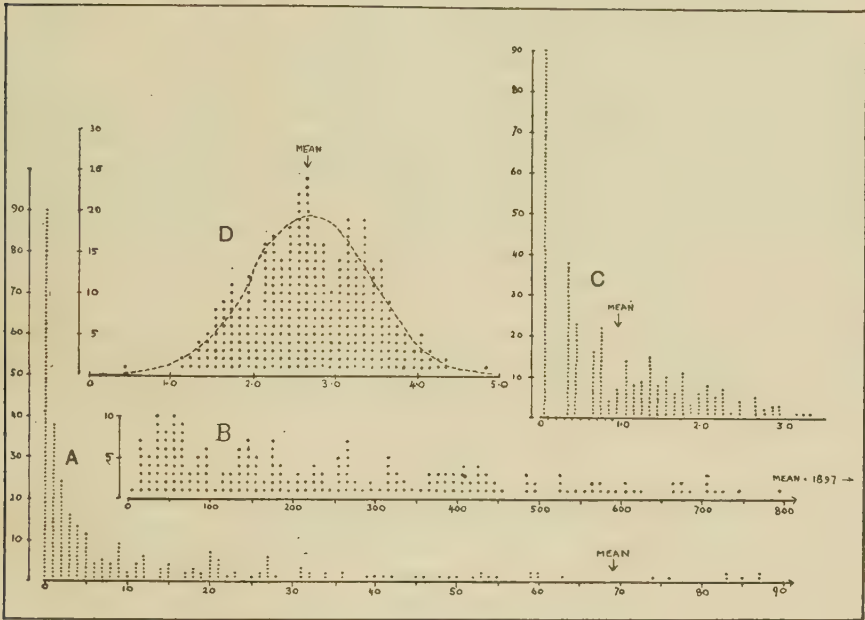
The shape of the curve of distribution of the catches is, however, not constant throughout the year, but changes from month to month. An examination of the results for each month separately has shown that the peak of the curve is at zero in March; at about 2 in April; about 5-9 in May; about 40-50 in June; about 80-90 in July; about 40-50 in August; 50-60 in September; about 11 in October; about 2-4 in November; and at zero again in December, January and February.

That is to say, that in the summer months there is a skew curve but in the winter the skewness has become so extreme that the portion below the peak at zero no longer exists. This is of course owing to the fact that it is not possible to catch a "fraction" of an insect in the trap. Theoretically the "zero" nights would include all nights on which conditions would lead one to expect between 0 and 1 insects (or only one insect in several traps).

To show this effect distinctly, fig. 3 has been prepared which gives the distribution in the three winter months (December, January and February) and the three summer months (June, July and August) of all four years together. Fig. 3, B shows the frequency distribution during the summer months for all catches below 800 per night arranged in groups of 10 units. The peak of the

curve is somewhere between 40 and 80 insects per night; the arithmetic mean of all catches is 1897. Fig. 3, A shows the distribution for the three winter months for all catches up to 90 in single units. The peak of this curve is at zero. Higher values of course continue in both these diagrams towards the right—in the case of the summer curve 3, B, up to a maximum of 73,000, which on the same scale would be approximately twenty-five feet away!

Fig. 3, D shows the frequency distribution of the logs ($n + 1$) of all the summer values, including all those off the previous diagram (3, B), and gives an almost perfectly normal distribution. The mean log value is 2.7 (exactly



3

FIG. 3.—Frequency distribution of catches of all insects :—

- A Three winter months in four years; expressed as numbers in units up to 90.
- B Three summer months in four years; expressed as numbers in groups of 10 up to 800.
- C Three winter months in four years expressed as $\log. (n + 1)$.
- D Three summer months in four years expressed as $\log. (n + 1)$ with superimposed normal curve of same area.

at the peak of the distribution) and the standard deviation is 0.716. From these data a normal curve of the same area has been calculated and superimposed as shown by the broken line. From this it will be seen how very closely the frequency distribution of $\log n + 1$ agrees with the curve of normal distribution during the summer months.

The winter values when transformed to logs do not give a distribution so obviously close to the normal, as is seen in fig. 3, C. The peak is at zero and the mean 0.9. It should be noted, however, that the high numbers at 0.3 and 0.4 are flanked by values with no representatives, and the large number of values at zero really represent (as has been mentioned above) all the fractional

values below one insect which cannot occur. Theoretically they would be spread out between 0 and — infinity.

It would appear, therefore, that the use of logs is an almost perfect transformation during the summer months when catches are high, but that it is not perfect (although at the same time much better than the actual numbers) during the winter months when dealing with low captures.

It follows from the above that if catches are at any time varying round a mean, then catches of twice the mean are as likely to occur as catches of half the mean; catches of three times the mean are as frequent as catches of one-third the mean; and so on.

As a result of the use of geometric means two valuable effects are obtained. First the swamping effect of occasional very large catches is greatly reduced, and secondly consistency in results is emphasised.

For example, a comparison was made (Williams 1937) between the total captures in the same trap on all the odd nights and all the even nights in the first three years. There can be no possible reason to expect a difference between these two sets of values yet, owing to the accidental distribution of a few very large captures, the arithmetic mean catch of the odd nights was 45% higher than that of the even nights. When the geometric mean was used the difference between the odd and even nights was reduced to 4.5%. Thus a difference of 45% in actual numbers after over 1000 nights (500 comparisons) was of no significance.

A second example may be quoted in the number of moths of the family NOCTUIDAE captured each night in the week of full moon and in the week of no moon, in October 1933 (see Williams 1936a) as shown in Table 3.

TABLE 3.

Catches of NOCTUIDAE in the week of full moon and the week of no moon in October 1933, on number and logarithm basis.

Day of week	Number		Log ($n + 1$)	
	No moon	Full moon	No moon	Full moon
1	2	0	0.48	0
2	4	0	0.70	0
3	0	1	0	0.30
4	0	62	0	1.80
5	10	0	1.04	0
6	3	0	0.60	0
7	3	0	0.60	0
Mean log	—	—	0.49	0.30
Mean no. per night .	3.1	9.0	2.1	1.0

It will be seen that on the arithmetic basis the mean catch in the full-moon week is 9 and in the no-moon week 3.1. The higher value for the full-moon week is, however, almost entirely due to the abnormal catch of 62 insects on one night (which was heavily clouded). When the log ($n + 1$) is used the geometric mean catch is found to be 2.1 insects in the no-moon week and 1 in the full-moon week; thus giving a higher value in the no-moon week. This latter result is consistent with a large number of other comparisons between full- and no-moon weeks.

On the other hand, when consistent differences are present, the use of logs shows them most distinctly. For example, the ratio of the arithmetic mean catches in the first and last periods of the night of all insects in 1933 was 49.0 to 26.3 (see Williams 1935 : 531), while the ratio of the geometric means was 7.3 to 3.6. The former is 182 : 100 and the latter 203 : 100, thus showing a greater difference with the logs, owing to consistent differences in the original figures.

Several other examples of the use of the technique are discussed in the paper already quoted (Williams 1937), and it is generally adopted in the remainder of this paper.

What is the catch ?

The catch in the light trap in any one night is a sample—as unbiased as possible—of the night-flying positively phototropic insects which are active in the neighbourhood of the trap. The area from which these are drawn is not known, nor is it likely that this area is the same for different species, or for the two sexes of the same species, or even for the same insect on different nights.

If the night is cold the majority of insects will be dormant and lie hidden away in sheltered places as they have during the day : the catch will then be small. If the night is warm there will be greater activity and a correspondingly greater catch. The catch therefore is directly affected by the state of activity of the insects.

If, on the other hand, the activity of the insects is the same on two nights, but the total number of insects in the district is different, then again the catch will alter.

The catch is therefore proportional to both the activity and the population of the phototropic insects; otherwise :—

$$\text{Catch} \propto \text{Activity} \times \text{Population.}$$

The activity is, however, affected by a number of different factors such as wind, rain, temperature, humidity, etc., each of which can apparently act independently of the others. Thus :—

$$\text{Total activity} = \text{activity due to temperature} \times \text{activity due to wind} \times \text{activity due to humidity etc.}$$

Therefore :—

$$\text{Catch} \propto [\text{act. T.} \times \text{act. W.} \times \text{act. RH. etc.}] \times \text{Pop.}$$

Since, however, proportional changes in the catch, as expressed by logs, are being dealt with almost entirely the result is :—

$$\log. \text{ catch} = [\log. \text{ act. T.} + \log. \text{ act. W.} + \dots] + \log. \text{ P.}$$

The log. catch is therefore made up of portions due to the effect on activity of the different environmental factors plus a portion determined by the total population available for sampling.

GENERAL SURVEY OF CLIMATIC FACTORS.

It is impossible to study insects in the field without realising to what a large extent their activity and abundance are determined by the effect of the various climatic factors of their environment. It is, however, a big step from the realisation that some of the factors have a large and some a smaller effect, to a proper analysis which will show on some scale of measurement exactly how

much effect is produced in the fauna by a particular extent of change in one particular factor of the environment.

One expects that if any change in a single factor, such as temperature, produces a change in the catch of the trap, then the size of the change in the catch (the dependent variable) will be in some way proportional to the change of the weather factor (the independent variable).

Thus in any locality where there is a big variation in temperature, the effect on the catch will be large; if, however, temperature changes in the environment are small, the effect will be small. If, however, it is possible to express the total effect in terms of the effect produced by *unit changes* in the independent factor, one will have a figure that can be used not only to compare effects from day to day in one locality but also to compare the effect of that factor in different localities where its variability is different and it is more or less influenced by other competing factors.

The object, therefore, is to attempt to express the effect of the weather factors of the environment on the catch (and later, on the population) as an integration of effect of a series of influences, the individual effect of each of which is a multiplication of the effect per unit change by the extent of the change.

The weather conditions which may be concerned can be conveniently grouped under six headings :—

- | | |
|------------------------|----------------------------|
| (1) Temperature. | (4) Wind. |
| (2) Radiation (Light). | (5) Atmospheric pressure. |
| (3) Moisture. | (6) Thunder and lightning. |

(1) *Temperature.*

Temperature is probably the most important single factor in the climate and weather of a locality such as Rothamsted, in the cool temperate zone (latitude 51° 50' N.). Temperatures are taken as part of the routine of the meteorological section, and the principal ones that have been considered are the maximum air temperature of the day previous to the catch and the minimum during the night of the catch, which normally occurs about dawn during the last of the eight periods into which the catch was automatically divided. These temperatures are taken in a screen at a height of about 4 feet from the ground and so almost exactly at the level of the trap.

The mean difference between these two, which is the "daily range," varies from 10° to 17.7° F. in different months, but this has not been found to have any very close connection with the catches in the trap (see pp. 246 and 268).

In addition to the above a minimum thermometer is exposed just above the surface of the ground, and the reading, known as the "grass minimum," gives a close measure of the lowest temperature to which the air in contact with the surface of the ground has fallen. The ground cools by radiation more rapidly on a clear night than on a cloudy night and so the differences between the air minimum and the grass minimum are related to the amount of cloud. Large differences are usually found on clear nights, while if the difference is 2° F. or less the night is certainly heavily clouded. Occasionally with complete cloud the grass minimum is a little above the air minimum.

It has been found undesirable as a general rule to consider the effect of temperature at any fixed hour, as the length of the night is continually varying and the 9 p.m. reading is, for example, in some months before the trap starts and in others after it has been working for several hours. However, in one

or two cases the effect of 9 p.m. temperature has been studied for June and July when the length of the night is varying less rapidly.

(2) *Radiation.*

The source of heat which alters the air temperature is, of course, radiation from the sun. The light from the sun does not directly affect the catches as trapping only starts after sunset and ends before sunrise. It will be shown later that there is a very slight tendency for good catches to follow days with more sunshine, but this is probably an indirect effect through temperature.

Moonlight has, however, a definite reduction effect on the catch, which has already been discussed in a previous paper (Williams 1936a). The catch is affected by both intensity and duration of moonlight. The duration of moonlight during the trap hours depends on the hours at which the moon rises and sets in relation to the hours of darkness. The intensity of moonlight depends upon the phase of the moon and on its angle above the horizon.

The time of rising and setting of the moon is on an average 49 minutes later each night, but the interval varies from 12 minutes to 1 hour and 33 minutes, and is of course not the same for rising and setting on the same night.

The amount of moonlight reaching the ground is much affected by the prevalence of cloud.

(3) *Moisture.*

In normal meteorological records rain is recorded as between 9 a.m. and 9 a.m. Thus any rain that falls up to 9 a.m. on one day is credited to the previous day. These figures may be misleading if attempts are made to use them in a calculation of the present type.

Rain is, however, measured at Rothamsted by recording instruments which give the time and amount of precipitation, and from these charts figures have been obtained for the rainfall from 6 a.m. to 6 p.m. and from 6 p.m. to 6 a.m. separately. These are known as the "day" and "night" rain.

The amount of water in the atmosphere can be expressed in three different ways:—

- (a) as the weight of water vapour in a given volume of air; usually expressed as grammes per litre;
- (b) as the vapour pressure of the water vapour, usually expressed in millimetres or inches of mercury;
- (c) as "Dew point," which is the temperature at which the particular amount of water in the air is sufficient to produce saturation.

In general, however, atmospheric moisture in biological work is not expressed in absolute units but in connection with temperature as either "Relative Humidity" or "Saturation Deficiency."

The former is a measure of the amount of water in the air in proportion to the total amount that would be required to produce saturation. The latter is the additional amount required to produce saturation.

Thus if VPT is the vapour pressure that would be required for saturation at the given temperature, and if VPD is the vapour pressure of saturation of the given air at the dew point, then

$$\text{Relative Humidity} = 100 \times \frac{\text{VPD}}{\text{VPT}}$$

and $\text{Saturation Deficiency} = \text{VPT} - \text{VPD}.$

The relation between Relative Humidity and Saturation Deficiency is linear

for a single temperature, but does not remain the same for a change of temperature.

Still another measure including both moisture, temperature and wind is "evaporation," but owing to the lack of any good standardisation of this in the meteorological observations it has not been used in the present work.

There have been for many years differences of opinion on the relative value for biological work of the use of Relative Humidity and Saturation Deficiency and this point will be discussed in the statistical analysis which follows.

Wet and dry bulb readings, from which both R.H. and S.D. values can be calculated, were taken at Rothamsted three times a day, at 9 a.m., 3 p.m. and 9 p.m. in the first year and a half of the trap work; but unfortunately in July 1934 the 3 p.m. and 9 p.m. readings were discontinued. Records after this date have to be calculated from recording hygrometers which were not very reliable. The relative humidity at midnight and after is nearly always over 90% even in the summer months.

Other factors associated with atmospheric humidity are cloud and fog.

Cloud, in addition to indicating high humidity, has two effects already referred to: (1) it prevents radiation of heat from the ground at night and so helps to keep up the night temperatures; (2) it keeps off radiation from the sun during the day and the moon during the night. Cloudy nights in general differ from clear ones in having lower maximum and higher minimum and grass minimum temperatures, but have about the same mean temperature. They have a much smaller daily range and a smaller difference between the screen minimum and the grass minimum.

Fog is only a special case of cloud at ground level, but in addition to indicating high moisture it has a new biological effect of interfering with visibility. It occurs usually on cold nights with clear sky in the winter, but occasionally warm fogs occur early in the autumn. (See p. 271.)

(4) *Wind.*

Wind is recorded at Rothamsted by a Dines Anemograph situated on the roof of the laboratory about 320 yards from the trap, the vane being at a height of about 70 feet.

The analysis of wind is made difficult by its rapid variation in strength, sometimes one part of a night being stormy and another part calm. This is particularly the case in winter, when nights frequently start stormy and become calm well after midnight. Fuller details will be found on p. 278.

(5) *Barometric pressure.*

Barometric pressure is recorded regularly, and for the purpose of most of the analyses below the days are divided into 9 categories, showing the interrelation of two sets of three factors: (A) barometer high, medium or low. (B) barometer rising, steady or falling. Full details will be found on p. 284.

(6) *Electrical phenomena.*

Thunder or lightning, or both, were recorded on forty occasions during the six summer months in the four years.

(7) *Interrelation of climatic factors.*

With so many possible factors the analysis of their effects is by no means likely to be easy, but the problem is unfortunately complicated even further by the close relation that many of them bear to one another.

In Table 3 an attempt has been made to summarise briefly some of these interrelations. A + indicates that the two factors rise and fall together; a — indicates that as one increases the other decreases.

Thus one may see, for example, that maximum temperature is positively associated with minimum temperatures, with the difference between minimum and grass minimum, with sunshine, and with the level of the barometer; but it is negatively associated with relative humidity, day rain, cloud and perhaps wind.

TABLE 4.
Interrelation of various weather factors.

	Max. temp.	Min. temp.	Min. g.m.								
Temperature, min. . . .	+										
Temperature, min.—G.M. . .	+	?—									
Sunshine	+	?—	+	Sun							
Moon (light reaching ground)	?	?	+	+	Moon						
Relative humidity	—	—	?	—	—	R.II					
Rain (previous day)	—	—	—	—	—	+	Day rain				
Rain (during night)	—	+	—	+	—	+	+	Night rain			
Cloud	—	+	—	?—	—	+	+	+	Cloud		
Wind	?+	+	?—	?—	—	?	?+	?+	+	Wind	
Barometer (level)	+	+	?	+	?+	—	—	—	—	—	

Minimum temperature, on the other hand, is positively correlated with night rain, cloud, wind and barometer.

Although the phases of the moon are regular and independent of weather conditions, yet the amount of moonlight reaching the earth (and hence any effect on the trap) is negatively correlated with relative humidity, night rain, cloud and wind and positively correlated with sunshine and the differences between minimum and grass minimum temperature.

Windy nights tend to have higher minimum temperature than calm nights, and this is particularly marked in the winter.

Thus it is almost impossible by simple means to get at the exact effect on the catch of each factor, independent of all others. The only method that seems capable of giving an answer is the statistical method of multiple partial regressions, which will be discussed later.

The simple relation of catch to any one factor is, however, often of considerable interest to the biologist, and the plan adopted will be to deal first with the direct relationships of single factors and then with the analysis of multiple effects.

COMPARISON OF NIGHTS OF HIGH AND LOW CATCH.

As a preliminary to a more detailed survey of single factors, it is interesting to make a comparison of the weather conditions prevailing on nights with unusually high or unusually low catch. To provide data for this the three nights with the highest catch and the three with the lowest in each of the months from May to October in each of the four years have been tabulated. That is to say, 72 good and 72 bad nights spread over the summers of four

years, each group containing approximately 10% of the total nights in that period.

TABLE 5.

Examples of the weather conditions on days with unusually high and unusually low catches in the summer of 1935.

Temperature. m.-g.m. = difference between screen minimum and grass minimum.
Night cloud. H = heavy cloud (over 90%), I = intermediate cloud (10-90%), L = light cloud (less than 10%).
Moon. a = after, b = before, N = new moon, F = full moon.
Wind. number in 6 groups as explained in text.
Barometer. R = rising, S = steady, F = falling; H = high, M = medium, L = low.

1935	High catch						Low catch					
	June		July		Aug.		June		July		Aug.	
	23	24	2	10	7	8	8	11	8	18	13	27
Catch, log. depart. from mthly. mean	+1.12	+1.20	+0.67	+0.80	+0.82	+0.89	-1.06	-1.01	-0.88	-1.32	-1.39	-1.07
Temperature:												
Max. . .	78.9	81.5	70.9	79.3	82.0	80.0	61.2	60.8	69.0	62.2	65.2	61.4
Min. . .	60.2	60.5	56.2	61.5	57.4	58.5	41.5	47.5	49.6	45.4	46.1	40.2
Grass min. .	52.3	57.6	53.3	55.8	51.3	54.3	34.1	43.4	40.8	40.7	38.4	33.3
Range . .	18.7	21.0	14.7	17.8	24.6	21.5	19.7	13.3	19.4	16.8	19.1	21.2
Min.-g.m. .	7.9	2.9	2.9	5.7	6.1	4.2	7.4	4.1	8.8	4.7	7.7	6.9
Night cloud .	L	I	I	L	H	H	L	L	L	L	L	I
Moon, pos. in cycle .	7aF	6bN	2aN	5bF	7bF	6bF	8aN	5bF	7bF	3aF	1bF	1bN
Wind, group .	1	1	3	1	1	1	2	5	1	1	1	1
Sun, hours .	14.3	15.2	8.6	12.8	9.1	5.3	13.1	5.6	13.9	2.5	11.5	5.3
Rain, day .	—	—	—	—	—	—	—	0.06	—	0.62	—	—
Rain, night .	—	—	—	—	—	0.05	—	0.01	—	—	—	—
Barometer .	MF	MF	HR	MR	MF	MF	MR	LR	HF	LS	MR	MF
Rel. humidity:												
Min. prev. day .	50	53	64	47	44	47	52	60	51	81	43	72
Sunset . .	80	80	85	66	64	59	68	95	76	94	62	88
9 p.m. . .	84	85	88	72	78	72	75	93	84	83	74	92
Midnight .	92	95	87	85	84	78	92	96	94	92	86	94
Sunrise . .	95	96	93	92	94	94	98	96	95	95	92	94
Max. of night .	95	96	93	92	94	94	98	96	95	95	92	94

Table 5 shows a sample of the data for 1935, including the departure of the log. catch from a 29-day running mean, various temperatures, and measures of cloud, moon, wind, sunshine, rainfall, barometer and relative humidity at various hours.

Tables 6, 7, and 8 show a summary of the average values of these factors on the best and worst nights for each year, in all four years, and the differences between the values. Figs. 4 and 5 show the frequency of occurrence of the values of certain of these factors in the two opposing types.

In the first place it will be seen from Table 6 that the average departures of the log. catch on all good nights is + 0.98 above normal, and on the bad nights - 1.02 below normal. Converted into numbers, this means that the 72 good nights have catches averaging almost exactly ten times the normal, and the 72 bad nights have catches almost exactly one-tenth of the normal. It may be noted in passing that this great similarity of log. departures for the two extreme groups, each containing 10% of the total observations, is a further strong argument for the validity of the use of logarithms in analysis.

In the maximum temperature the good nights average about 9° F. above the bad nights with somewhat similar variability in each group (fig. 4, A).

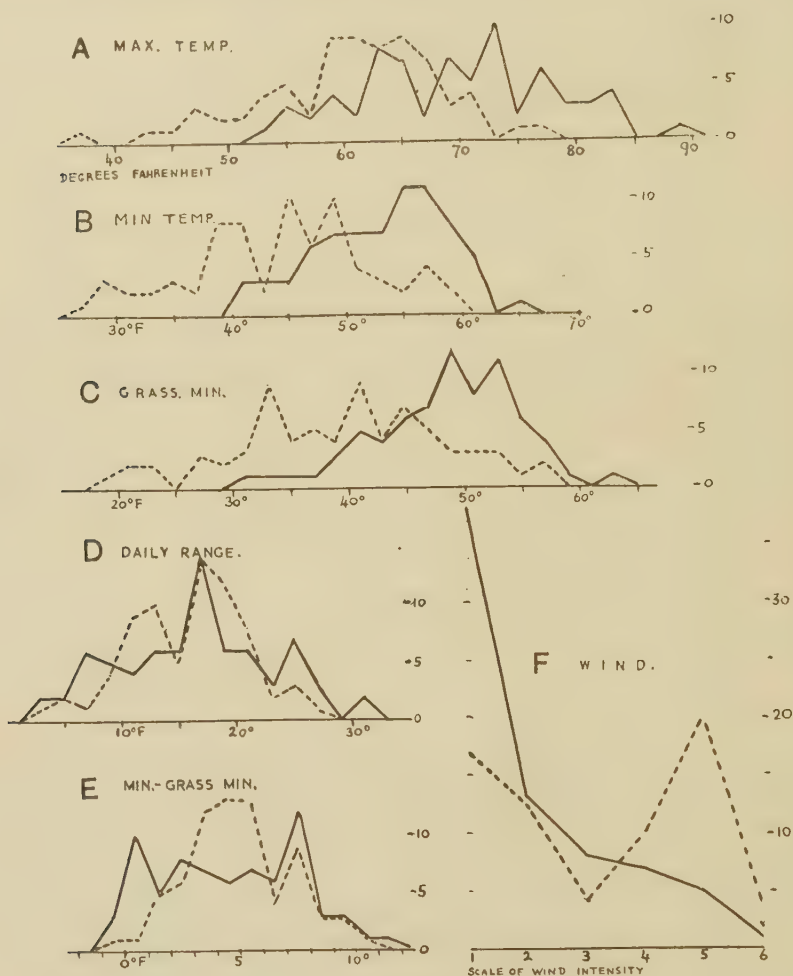
In the screen minimum temperature the good nights average 9.5° F. above the bad nights, but it will be seen from fig. 4, B that, in addition to the difference

TABLE 6.
Difference between certain weather conditions on nights of high and low catch in six summer months in all four years.

Year	Catch	Temperature					Night cloud			Sun Hours	Rain					
							No. of days				Day		Night			
		Max.	Min.	Grass min.	Daily range	m.-g.m.	Clear	Int.	Cloudy		Tot.	No. of days	In. per day	Tot.	No. of days	In. per day
Best nights :																
1933	+0.99	71.5	54.3	49.5	17.5	4.8	3	7	6	7.2	2	0.15	4	—	0.07	—
1934	+0.89	70.7	53.5	49.2	17.2	4.3	3	9	6	5.6	1	0.01	3	—	0.12	—
1935	+1.11	70.2	52.0	47.3	17.6	4.7	4	7	6	6.7	4	0.76	5	—	0.71	—
1936	+0.91	65.2	51.9	47.7	13.5	4.2	1	7	10	4.1	4	0.69	6	—	0.56	—
4 years	+0.98	69.4	52.9	48.4	16.5	4.5	11	30	28	5.9	11	1.61	18	0.15	1.46	0.08
Worst nights :																
1933	-1.09	63.0	47.2	43.1	15.8	4.1	5	10	3	6.8	9	0.60	4	—	0.17	—
1934	-0.89	60.3	42.8	37.6	17.5	5.2	13	0	3	4.5	7	1.10	5	—	0.79	—
1935	-1.04	58.5	41.6	35.7	16.9	5.9	11	6	0	6.2	7	0.99	4	—	0.60	—
1936	-1.05	59.0	45.4	41.1	13.6	4.3	8	6	4	3.8	11	1.45	6	—	0.49	—
4 years	-1.02	60.2	43.4	39.4	16.0	4.9	37	22	10	5.3	34	4.14	19	0.12	2.05	0.11
Difference :																
1933	+2.08	8.5	+10.5	+6.4	+1.7	+0.7	—	—	—	+0.4	—	—	—	—	—	—
1934	+1.78	10.4	+10.7	+11.6	-0.3	-0.9	—	—	—	+1.1	—	—	—	—	—	—
1935	+2.15	+11.7	+10.4	+11.6	+0.7	-1.2	—	—	—	+0.5	—	—	—	—	—	—
1936	+1.96	6.2	+6.5	+6.6	-0.1	-0.1	—	—	—	+0.3	—	—	—	—	—	—
4 years	+1.99	9.2	+9.5	+9.0	+0.5	-0.4	-26	+8	+18	+0.6	-23	—	-1	—	—	—

in the average value, the minimum temperatures on the good nights are distinctly less variable than those on the bad nights.

The conditions of "grass minimum" temperature closely resemble those of minimum temperatures, with a mean difference of 9° F., and with less variability on the good nights (fig. 4, C).



4

FIG. 4.—Frequency distribution of occurrence of various weather conditions on nights of unusually high catch (solid line) and on nights of unusually low catch (dotted line) during six summer months (May to October) of four years.

The mean daily range (fig. 4, D) on good nights is almost identical with that on bad nights, but their distribution is different. The ranges on the bad nights are more closely grouped about the mean and less variable than the ranges on good nights.

In the difference between the screen minimum and the grass minimum (fig. 4, E), which (as has been explained) is a measure of the radiation of heat from the earth during the night, there is again practically no difference between

the average value on the good and bad nights, but the distribution is very different. The values on the poor nights are mostly grouped round the mean, whereas on the good nights there is evidence of two peak values, one with practically no difference between the two minima and the other at a difference of about 8° F. The former are nights of heavy cloud; the latter are apparently relatively clear nights in which the high catch has been produced by exceptionally high minimum temperatures probably following very hot days.

The distribution of night-cloud is quite different in the two types of night (Table 6). The 72 good nights include 28 with over 90% cloud and only 11 with less than 10% cloud. The poor nights, on the contrary, include only 10 with more than 90% cloud and 37 with less than 10%.

The wind for the purpose of comparison has been grouped into six artificial categories with maximum velocities during the night as follows: (1) nil, (2) less than 2 m.p.h., (3) 2-5, (4) 5-10, (5) 10-20, and (6) over 20 m.p.h. (see p. 278).

Table 7 and fig. 4, F show the frequency distribution of the different wind forces on good, on bad and on all nights. It will be seen that, as might be expected, dead calm conditions are much more frequent on the good nights and winds of over 10 m.p.h. more frequent on the poor nights. It is curious to note, however, that with a wind as slight as group 2 (under 2 m.p.h.) there is little or no difference between the good, the bad and normal nights.

The effect of moon has already been discussed in a previous paper (Williams 1936a). Fig. 5, G shows graphically how the good and poor nights are distributed according to the position in the lunar cycle. It will be seen that the good nights are more frequent in the new-moon half of the cycle and the bad nights in the full-moon half.

TABLE 7.

Frequency of occurrence of different wind intensities on nights of high and low catch.

	Wind group					
	1	2	3	4	5	6
Best nights . . .	38	13	8	7	5	1
Worst nights . . .	17	12	4	10	25	4
All nights . . .	26	11	8	11	11	2

Table 6 shows that the days preceding good nights have an average of about 0.6 hours more sunshine than the days preceding poor nights. The difference is small and of doubtful significance, but it should be noted that each of the four years taken separately shows a positive difference in favour of good nights. Fig. 5, H indicates that there is little or no difference in distribution and with such a large range the small difference is inconspicuous.

The sunshine problem is connected with that of rainfall which shows an interesting difference.

Separate figures are fortunately available for rainfall during the twelve day-hours 6 a.m. to 6 p.m. and during the 12 night-hours 6 p.m. to 6 a.m. Table 6 shows that night rain occurred on 18 of the best nights (with an average fall of 0.08 inches per night) and on 19 of the worst nights (with an average of 0.11 inches per night). There is practically no difference in these.

In the 12 hours daytime preceding the catch, however, rain fell on only 11 of the 72 best nights, but on 34 of the worst nights; that is, practically

half of the worst nights followed days with rain. Therefore it appears that rainfall during the daytime is associated with a low catch on the following night, but rain which falls during the night seems to have little or no effect.

The distribution of the good and bad nights in different conditions of barometric pressure is shown in Table 8. The barometer is divided into 9

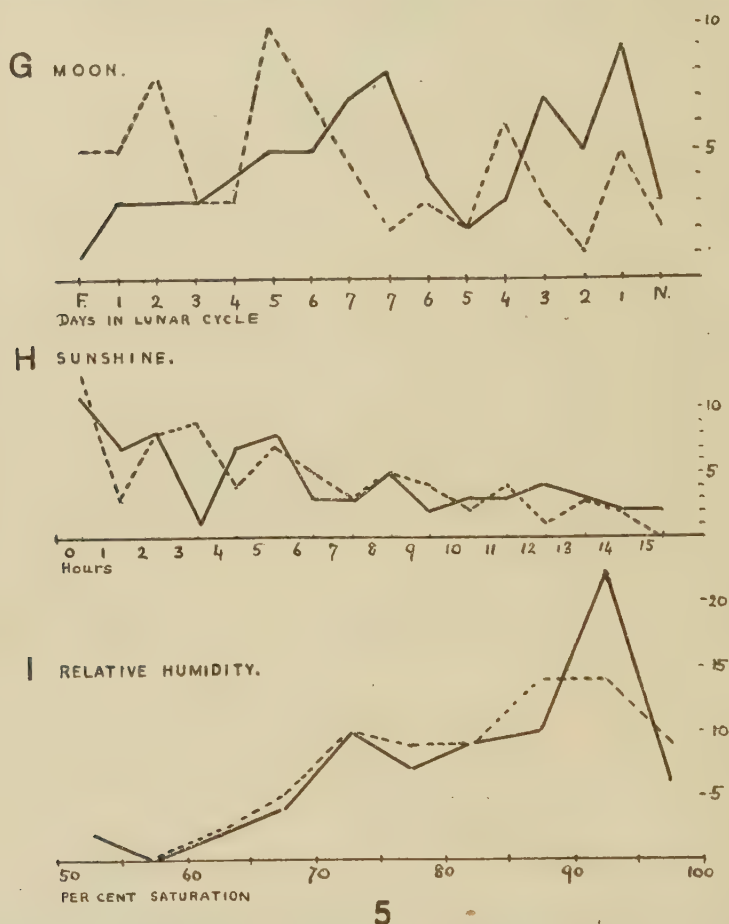


FIG. 5.—Frequency distribution of occurrence of moon phase, sunshine and relative humidity on nights of unusually high catch (solid line) and unusually low catch (dotted line) during the six summer months (May to October) of four years.

TABLE 8.

Frequency of occurrence of different barometrical conditions on nights of high and low catch.

	Best				Worst				Difference (best - worst)			
	R	S	F		R	S	F		R	S	F	
High .	8	11	1	20	2	2	3	7	+ 6	+ 7	- 2	+13
Medium .	8	16	22	46	11	8	15	34	- 3	+ 8	+ 7	+12
Low .	3	2	1	6	18	6	7	31	-15	- 4	- 6	-25
	19	29	24		31	16	25		-12	+13	- 1	

categories according to whether it is on the one hand high, medium or low, and on the other hand rising, steady or falling.

An examination shows that high catches are more frequently associated with a high barometer if rising or steady, and with a medium barometer if steady or falling; low catches are associated with low barometer either rising, falling or steady, with a medium barometer if rising, and unexpectedly, with a high barometer if falling. This latter point will be discussed more fully later (see p. 284).

If only the height of barometer is considered, good catches are more frequent with high or medium barometer and poor catches with low barometer. If only the direction of movement is considered, low catches are more frequent with a rising barometer, high catches with a steady barometer, and both are equally frequent on a falling barometer.

The problem of atmospheric humidity is particularly complicated as there are so many ways by which the results can be expressed. Table 9 shows a summary of comparisons of Relative Humidity at different times of the day and night. These include the minimum humidity of the previous day, the humidity at sunset, 9 p.m., midnight, sunrise and the maximum humidity during the night. In no case is there any significant difference between the good nights and the bad nights.

It might be inferred from this that there is no selection of damp or dry nights for high insect activity. This interpretation is not, however, correct. It has already been shown that the best nights are about 9° F. warmer than the poorest nights. Warm nights, however, have on an average a lower relative humidity than cool nights. Since there is *no* difference in the average relative humidity between the good (warm) nights and the poor (cold) nights it follows that good nights must be associated with the damper of the warm nights and poor nights with the dryer of the cool nights. Therefore the absence of a difference in relative humidity indicates a selection of nights of higher relative humidity for high activity (see p. 268).

TABLE 9.

Conditions of relative humidity at different times of night on nights of high and low catch.

Year	Min. prev. day	Sunset	9 p.m.	Midnight	Sunrise	Max.
Best nights						
1933 . . .	—	—	79	—	—	—
1934 . . .	58	69	78	83	87	90
1935 . . .	62	79	86	89	94	94
1936 . . .	75	87	91	95	95	97
4 years . .	65	78	84	89	92	94
Worst nights						
1933 . . .	—	—	80	—	—	—
1934 . . .	62	74	78	90	93	95
1935 . . .	60	78	85	90	94	95
1936 . . .	71	86	90	95	95	97
4 years . .	64	77	83	92	94	96
Difference						
1933 . . .	—	—	-1	—	—	—
1934 . . .	-4	-5	0	-7	-6	-5
1935 . . .	+2	+1	+1	-1	0	-1
1936 . . .	+4	+1	+1	0	0	0
4 years . .	+1	+1	+1	-3	-2	-2

THE GENERAL METHODS OF ANALYSIS OF THE INFLUENCE OF A SINGLE FACTOR,
AND THE RELATION OF TOTAL CATCH TO MINIMUM TEMPERATURE.

In order to explain the various problems in connection with the mathematical analysis of the influence of a single factor on the catch in the light trap, it is necessary to give a number of examples of typical methods and results. It has been thought desirable to use for this discussion examples relating to the action of minimum night temperature on total catch, so that this section will include both the discussion of methods and of the effect of this factor of the environment.

Before discussing other problems an attempt will be made to explain the exact meaning of the terms "regression," "correlation" and "variance" which are the bases of most of the analyses to follow, so that the reasoning can be followed by entomologists and others who are not specially familiar with statistical methods and nomenclature.

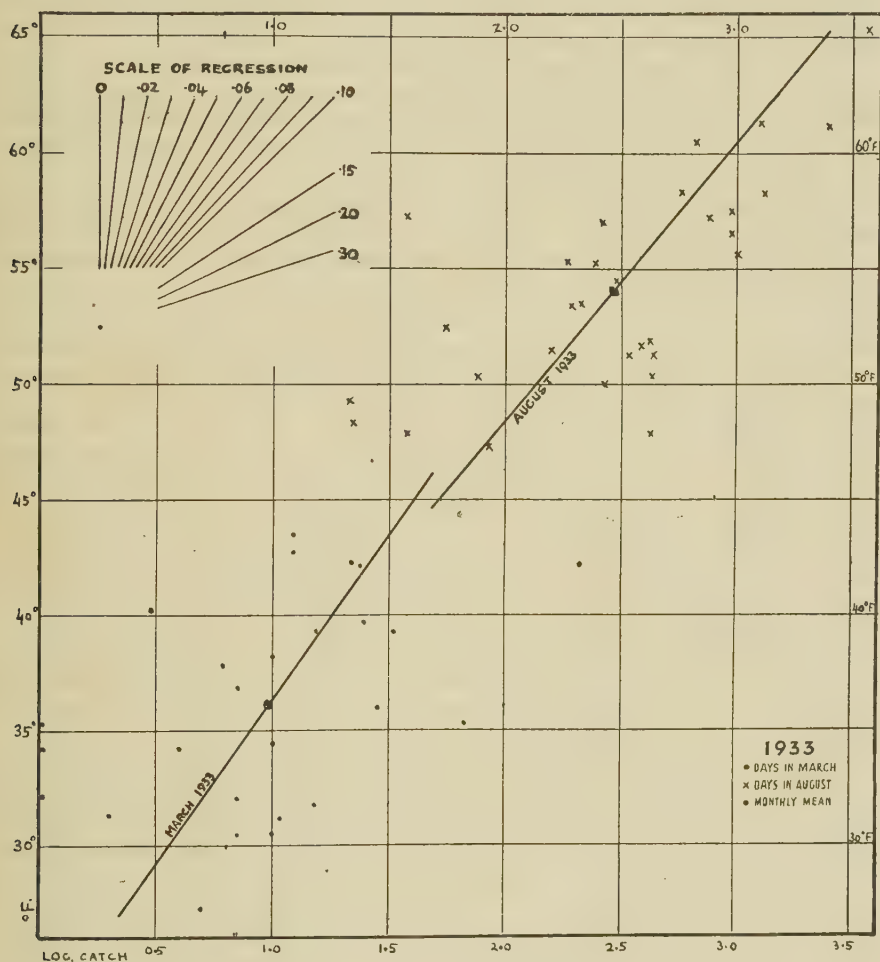
Table 10 shows—as an example—the catch, the log. catch, and the minimum temperature on each night of the months of March and August 1933. It will be seen that in March the mean log. catch was 0.97 and the mean minimum

TABLE 10.

Catch, log. catch and minimum temperature on the nights in March and August 1933.

Date	March 1933			August 1933		
	Catch	Log. catch	Min. temp.	Catch	Log. catch	Min. temp.
1	31	1.51	39.3	424	2.63	50.3
2	208	2.32	42.3	3596	3.56	65.3
3	—	—	—	1249	3.10	61.4
4	—	—	—	569	2.76	58.4
5	—	—	—	262	2.42	57.0
6	66	1.83	35.4	2500	3.40	61.2
7	9	1.00	34.5	661	2.82	60.5
8	22	1.36	42.1	371	2.57	51.6
9	27	1.45	36.0	992	3.00	55.6
10	6	0.85	36.8	235	2.37	55.2
11	3	0.60	34.3	192	2.29	53.3
12	6	0.85	32.1	74	1.88	50.4
13	2	0.48	40.2	209	2.32	53.5
14	9	1.00	38.3	939	2.97	57.5
15	11	1.08	43.5	179	2.26	55.3
16	11	1.08	42.8	83	1.92	47.3
17	5	0.78	37.9	35	1.56	57.3
18	14	1.18	39.3	54	1.74	52.5
19	—	—	—	159	2.20	51.5
20	4	0.70	27.3	20	1.32	49.5
21	10	1.04	31.2	21	1.34	48.4
22	0	0	34.3	267	2.43	50.0
23	0	0	32.1	35	1.56	47.9
24	1	0.30	31.3	432	2.64	51.4
25	—	—	—	420	2.62	51.8
26	9	1.00	30.5	335	2.53	51.3
27	14	1.18	31.8	740	2.87	57.3
28	6	0.85	30.5	949	2.98	56.5
29	23	1.38	39.7	1295	3.11	53.3
30	0	0	35.3	426	2.63	47.8
31	21	1.34	42.3	301	2.48	54.5
Mean	20	0.97	36.2	581	2.46	54.2

temperature was 36.2° F.; while in August the values were 2.46 and 54.2° F. respectively. It will also be seen that in general the larger catches are on the warmer nights and the smaller catches on the cooler nights. The night of the largest catch in August—3596 insects on the 2nd of that month—had a minimum temperature of 65.3° F., which was the highest experienced in all the four years of work.



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FIG. 6.—Scatter diagram and regression lines showing relation of log. catch of all insects and minimum temperature of the nights in March and August 1933.

The results can be expressed graphically in the form of a "scatter diagram" for each month. In this (fig. 6) each night is represented by a dot in the position corresponding to its correct minimum temperature and log. catch. There are for March, 26 dots (five days were missing) in the lower portion of the figure, with a larger dot representing the mean catch and mean minimum temperature for the month. It will be seen that the dots are spread over an area elongated

in a direction which indicates that, as a general rule, the higher the minimum temperature the larger the catch.

Through such a diagram it is possible to draw a line along the axis of this area which is a "best fit" to the points. If the points are close to a straight line—that is to say, if the influence of temperature is very definite and uncomplicated by other effects—the line may be fitted easily by eye. But if (as is more usual) the dots are scattered, the line can be best fitted in by calculation, and is known as the line of regression. The method of calculation will be found in any elementary book of statistics.

The regression line, as found by calculation, has been fitted to each of the two months shown in fig. 6. It indicates the average rate of change of catch (the dependent variable) per unit change of temperature (the independent variable). The calculated regression is the value which most closely explains the available data and leaves the least variation to be explained (or perhaps not explained!) by other sources of influence not considered at the moment.

For example, in fig. 6 the calculated regression of log. insect catch on minimum temperature for March is $+0.052$. In other words, the data given for March are most completely explained on the assumption that a rise of one degree Fahrenheit in the minimum temperature is associated with an increase of 0.052 in the log. catch; and, of course, each degree of fall in temperature is associated with a corresponding fall in the catch.

The regression for August is $+0.084$, showing that, from the data available, a degree rise in August 1933 is apparently associated with a greater increase in catch than a degree rise in March of the same year. Whether these figures are significantly different will be discussed later.

Since an increase of 0.301 on the log. represents a doubling of the catch at any level, the above figures can be restated by saying that in March 1933 the catch would be doubled with an increase of 6° F. in the minimum temperature, and in August 1933 with an increase of 3.6° F.

The angle of the line of regression, when expressed graphically, alters as the value alters, and an angular scale has been added to fig. 6 to illustrate this. The values on this scale, of course, depend on the relative scales of the horizontal and vertical co-ordinates.

A second value that can be calculated from the figures is the "correlation" between the two sets of values. This is to a certain extent a measure of the closeness of fit of the individual points to the regression line. A correlation of $+1.0$ shows that the relation between the two factors is complete, *i.e.* all the points are exactly on the regression line, and that as the value of one factor rises the other rises in exact proportion. A correlation of $+0.5$ indicates that the points are somewhat scattered. A correlation of 0 indicates that there is no evidence of relation between the two factors. Negative correlations indicate that as one factor rises the other falls.

For example, the points for August 1933 in fig. 6 give a correlation of $+0.68$; those for March, which are more scattered, give a lower value of $+0.43$.

The significance of the correlation depends on the number of pairs of values from which it is calculated. The fewer the values the higher must be the correlation for the same significance. In the present analyses most of the figures have been grouped in months with about 30 or 31 days. For this number of observations a correlation must be above ± 0.35 to have a probability value of 0.05 (*i.e.* only once in twenty repetitions might the results be

obtained by chance), or above ± 0.41 to have a probability of 0.02 (*i.e.* only once in 50 repetitions might it be obtained by chance).

If two months are grouped together (*i.e.* sixty observations) then the correlation values having the same significance are 0.25 and 0.29. In other words, the same correlation on a larger number of observations becomes more significant, or less likely to be due to chance.

Variance is a measure of the variability of a factor and, mathematically, is the sum of the squares of the departures of the individual values from the mean. Thus in Table 11 the departures of the log. catch from the monthly mean on the first three days of June 1933 are -1.16 , -0.23 and -0.01 respectively. The total variance for the three days is, therefore, the sum of the squares of these values or $1.3456 + 0.0529 + 0.0001 = 1.3986$. Variance is always positive.

Covariance is a measure of the degree of interrelation of the simultaneous departures from the mean of two different variables, and is obtained by cross multiplying the two departures. On the first three days of June 1933 the departures from the monthly mean of the minimum temperatures were -5.0 , 0.7 and 0.6 . Thus from the figures already given above it will be seen that the covariance between catch and minimum temperature for the three days is

$$(-1.16 \times -5.0) + (-0.23 \times 0.7) + (-0.01 \times 0.6) = 5.800 - 0.161 - 0.006 = +5.633.$$

Covariance is positive when the departures are both positive or both negative, and negative if the departures are of opposite signs.

These expressions, "regression" and "correlation," "variance" and "covariance," will be frequently used and it is important that a proper understanding of their meaning and limitations should be obtained.

When calculating a correlation or regression between the catch and a single arbitrarily selected factor of the environment, such as minimum temperature, it must be understood that the result obtained is really the effect on the catch of minimum temperature together with that of any other factor which is itself correlated with both catch and minimum temperature.

Thus it will be seen later that wind is positively correlated with minimum temperature and is negatively correlated with catch. Therefore if one makes a correlation or regression of minimum temperature with catch and neglects wind, one gets a value that will include the adverse wind effect and so will be smaller than the true temperature effect from which the wind has been eliminated. This problem will be taken up again later in the discussion of the simultaneous effect of two or more factors (see p. 288).

It should also be noted that the presence of a high correlation between two factors, or the possibility of calculating a significant regression, is in no way a proof that one factor is *directly* influencing the other. In the case above I have shown a significant correlation between the minimum temperature of the night and the number of insects caught. I infer from other knowledge that the probable explanation is that the higher night temperature is the cause of the high catch; but the purely mathematical process would lend just as much support to the idea that the large catch was the cause of the warm night! It is also possible, and frequently the true explanation, that the relation between the two correlated factors is not one of direct cause and effect, but that both are correlated with a third factor which has not appeared on the data provided.

Significant correlations and regressions, therefore, indicate a relationship,

but do not prove whether it is direct or indirect, or in which direction it is acting.

Two problems have next to be settled.

1. In what mathematical form are the catches to be expressed? Whether as actual numbers; as square roots; as logarithms; or by some other method?

2. Should the above values be used as they stand or should they be expressed as a departure from some fixed or changing mean, or as a difference between pairs of values? In this connection the possibilities are very numerous, but the following have been tested:—

- (a) Values expressed as they stand.
- (b) Values expressed as departures from a fixed monthly mean.
- (c) Values expressed as departures from polynomial curves.
- (d) Values expressed as departures from 31-, 29-, 15- and 5-day running means.
- (e) Values expressed as differences between successive pairs of nights.

With reference to the first problem, I originally started calculations in this investigation using the numbers themselves, next I tried square roots, and finally abandoned these in favour of logarithms. The arguments for this have already been given (p. 234 and Williams 1936a and 1937). In the discussion below, therefore, logs will be used almost entirely.

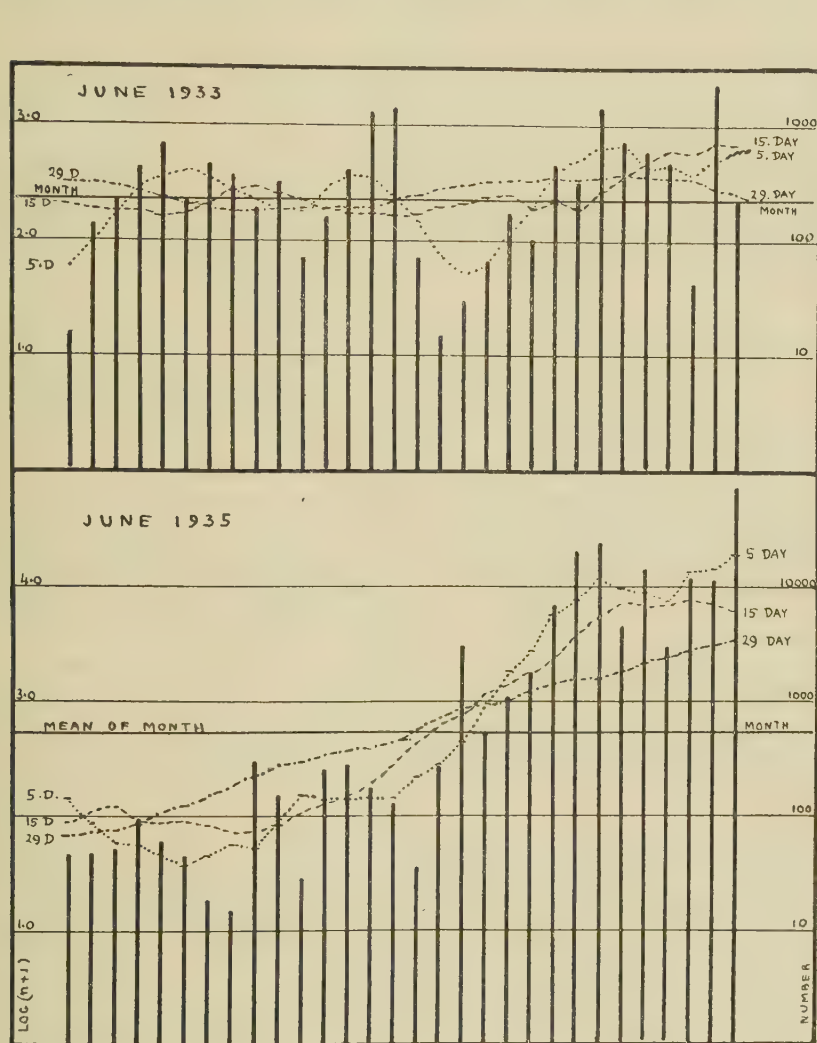
It is, however, important to note that because the logarithmic transformation has been found the most suitable for the present problem, which deals

TABLE 11.

Catch, log. catch and departures of log. catch from various means in June 1933.

Date	Actual catch (<i>n</i>)	Log. catch log (<i>n</i> + 1)	Departures from means								Diff. between successive days	
			Monthly (fixed)		29-day (running)		15-day (running)		5-day (running)			
			+	—	+	—	+	—	+	—	+	—
1	15	1.20		1.16		1.30		1.10		0.57	0.93	
2	134	2.13		0.23		0.37		0.14	0.20		0.22	
3	224	2.35		0.01		0.12	0.10		0.13		0.26	
4	406	2.61	0.25		0.20		0.37		0.16		0.22	
5	676	2.83	0.47		0.46		0.63		0.28			0.51
6	209	2.32		0.04		0	0.09			0.28	0.32	
7	431	2.64	0.28		0.36		0.33		0.11			0.06
8	379	2.58	0.22		0.33		0.16		0.12			0.32
9	187	2.27		0.09	0.02			0.19		0.10	0.23	
10	313	2.50	0.14		0.24		0.10		0.22			0.66
11	68	1.84		0.52		0.46		0.51		0.44	0.36	
12	159	2.20		0.16		0.09		0.08		0.25	0.40	
13	400	2.60	0.24		0.30		0.36		0.04		0.50	
14	1250	3.10	0.74		0.81		0.92		0.54		0.04	
15	1389	3.14	0.78		0.78		0.96		0.81			1.29
16	69	1.85		0.51		0.56		0.38		0.30	0.67	
17	14	1.18		1.18		1.30		1.13		0.71	0.31	
18	30	1.49		0.87		1.10		0.83		0.22	0.32	
19	63	1.81		0.55		0.72		0.57	0.03		0.41	
20	165	2.22		0.14		0.30		0.18		0.15		0.22
21	98	2.00		0.36		0.53		0.28		0.10	0.65	
22	448	2.65	0.31		0.12		0.30		0.08			0.05
23	396	2.60	0.24		0.07		0.32			0.09	0.56	
24	1460	3.16	0.80		0.62		0.75		0.36			0.31
25	714	2.85	0.49		0.34		0.30		0.04			0.10
26	563	2.76	0.39		0.21		0.05		0.14			0.06
27	493	2.69	0.33		0.15			0.09	0.04			1.08
28	40	1.61		0.75		0.92		1.17		0.94	1.72	
29	2119	3.33	0.97		0.87		0.48		0.63			0.97
30	229	2.36		0		0.05		0.48		0.50	1.16	
Variance (= sum of squares)			9.029		10.080		9.369		4.228		12.307	
Variance for June, 1935			33.456		12.449		7.369		4.513		9.396	

with varying catches in a light trap, it does not follow that it is suitable for other sets of figures. The main test of its suitability is that it reduces the frequency distribution curve of the data to an approximately normal and symmetrical form as already shown in fig. 3.



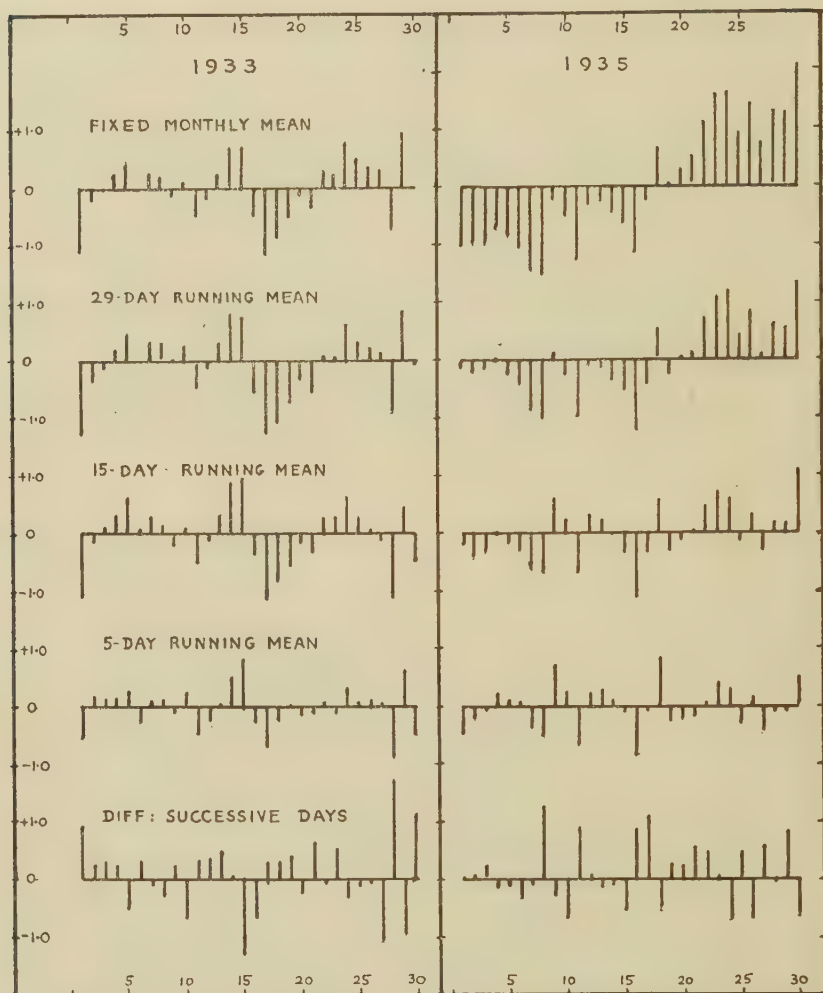
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FIG. 7.—Histograms of log. catch of all insects in June 1933 and June 1935 with various means to indicate relation of mean to night's catch, and the effect on means of the definite trend in 1935.

Returning now to the question of the expression of catch and temperature as absolute values, as departures from fixed or running means, or as differences; some of the different possibilities of treatment for the same set of observations are shown in Table 11 and figs. 7 and 8. The table shows the value for the catch of insects each night in June 1933 expressed as a number (n) and as log.

($n + 1$); and the logs. are further shown as departures from a fixed monthly mean, from running means of 29, 15 and 5 days and as differences between successive days. It should be noted that the latter gives a value equal to twice the departure from a 2-day running mean.

Three points must here be emphasised. First, that whatever method is



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FIG. 8.—Departure of night's catch from various means in June 1933 and June 1935 to show methods of eliminating the trend of catch in 1935.

selected both variables must be treated by the same method. Thus if log. catch is expressed as departures from a 5-day mean, the minimum temperature must also be expressed in the same way.

Secondly, that the use of running means requires information of the values of catch and temperature outside the exact period to be dealt with. Thus the departures from a running 29-day mean for May can only be calculated if the

values for the second half of April and the first half of June are known. Thus more information is analysed with a long-period running mean than with a short-period running mean or with a fixed mean.

Thirdly departures from a fixed mean (*e.g.* monthly mean) give within a single month the same correlations and regressions as the actual values themselves over that period.

The total variation to be explained in each case (statistically speaking the "variance") is shown at the foot of Table 11. From this it may be seen that the variance in June 1933 is greatest for departures from fixed monthly means and from 29-day running means, and smallest for departures from 5-day means. If one divides the variance for the difference between successive days by 4 (since each difference is twice the departure from a 2-day running mean) one finds that this value is again smaller than the 5-day mean value. Thus the shorter the period of the running mean the less the variance. This will be seen also from fig. 7, which shows how the shorter period means follow more closely the variations in the catches.

The difference between the variance for the fixed monthly mean and the running mean depends largely on whether there is any definite trend in the values over the period under consideration.

In June 1933 there was no definite trend in the catch (see fig. 7) so that the variance from the fixed monthly means and from running 29-day means are almost the same. In June 1935 (see also fig. 7) there was on the contrary a very definite trend in the catch from low values at the beginning of the month to very high values at the end. This is immediately reflected in the variance as shown on the bottom line of Table 11. The variance from fixed monthly means is 33.456 in 1935 (*cf.* 9.029 in 1933) while that from the 29-day running mean is only 12.449 (*cf.* 10.080 in 1933).

The way in which the trend is eliminated by short-term means or successive differences is best seen in fig. 8, which shows graphically the departures from the mean for June 1933 (no trend) and June 1935 (very definite trend). The trend in 1935 is obvious in the monthly means and the 29-day running means, noticeable in the 15-day means (particularly at the beginning and end of the month) but is eliminated in the 5-day means and in successive differences.

Thus if fixed means are used for calculation the variance due to trends is included; if long-term running means are used variance due to steady trends is at least partly eliminated; if short-term running means are used variance due to both shorter and longer trends is eliminated. If there is a simultaneous trend in the same direction in both dependent and independent variables, the use of fixed means will tend to exaggerate both correlation and regression; if the trends are in the opposite direction the correlation and regression will be correspondingly diminished.

With short-term running means, however, much less of the total variation is discussed and there is a possible danger of omitting useful evidence by considering it as a trend rather than an immediate effect of the factor concerned. It is here that general knowledge of the problem has to be the deciding factor.

In the present case I believe that the long-period trends seen in the catch as it changes from month to month are largely a "total population" effect; while the rapid changes from night to night are much more definitely the effect of weather conditions in altering activity. If this is so, more accurate measurements of the effect of a factor (such as minimum temperature) on the *activity*

of insects will be obtained by the use of departures for a short-period running mean or from the difference between successive days.

One statistical difficulty, connected with the significance of the results, should, however, be pointed out here. If one uses the thirty catch values in one month as departures from a fixed- or long-period running mean one obtains a result the significance of which is based on 29 degrees of freedom. If, however, one takes the difference between successive days the fifteen values for the day differences 1-2; 3-4; 5-6 etc. are independent of each other and so are the values 2-3; 4-5; 6-7, but the two series are not independent. So that while the significance of the resulting regression can be calculated from either half set of differences (each with 14 degrees of freedom), the result based on all the possible differences, although more accurate than either half set, cannot be considered as if it were based on twice as many degrees of freedom.

Polynomial means of the third and fourth degrees were calculated for the catch and minimum temperatures for June 1933, but only based on the square root of the catch, and not on the log. No advantage seemed to be gained by their use and they suffered from several practical disadvantages as follows: firstly the long time necessary for the calculation; secondly the shape of the polynomial curve near each end depends on how many values were taken on either side of the series; and thirdly polynomial curves calculated separately for two successive months do not "join up," so that the mean on the last day of one month is quite different from that of the first day of the next month. For these reasons no further calculations were made on this basis.

TABLE 12.

Correlations and regressions between log. catch and minimum temperature for the same months calculated from different means.

	June				July	
	1933		1935		1933	
	Cor.	Reg.	Cor.	Reg.	Cor.	Reg.
Departures from—						
Monthly mean . . .	0.73	0.123	0.77	0.161	0.29	0.068
29-day running mean . . .	0.61	0.091	0.52	0.094	0.34	0.075
15-day running mean . . .	0.74	0.110	0.44	0.062	0.34	0.064
5-day running mean . . .	0.59	0.107	0.37	0.051	0.15	0.021
3-day running mean . . .	0.65	0.109	0.25	0.043	—	—
Difference between successive days	0.71	0.100	0.36	0.051	0.24	0.025

Regressions and correlations have not been calculated by all these methods for all the 48 months; they have, however, all been done for the three months June and July 1933 and July 1935, and in addition calculations have been made from a running 3-day mean. These are all shown in Table 12.

The effects of the different methods in each month vary considerably and are difficult to understand. Some of them are accidental, due to the relatively small number of observations. It is, however, easy to see, in June 1935, the effect of the simultaneous trend from low to high values in both catch and minimum temperature, which causes an abnormally high regression when departures from a fixed monthly mean are used.

The essential differences between the use of departures from a fixed monthly mean as one extreme, and the differences between successive days as the other,

in the calculation of correlations and regressions is shown in Tables 13 and 14 and in fig. 9.

Table 13 shows the regressions and correlations of log. catch and minimum temperature calculated from departures from monthly means for each of the 48 months separately; for the four repetitions of each month; for each of the four years; and for the four years together.

TABLE 13.

Correlations and regressions of log. catch on minimum temperatures from departures from monthly means.

	1933-34		1934-35		1935-36		1936-37		All 4 years	
	Cor.	Reg.	Cor.	Reg.	Cor.	Reg.	Cor.	Reg.	Cor.	Reg.
March .	0.43	0.052	0.45	0.056	0.65	0.098	0.53	0.064	0.54	0.070
April .	0.57	0.063	0.34	0.031	0.38	0.048	0.78	0.100	0.52	0.058
May .	0.43	0.111	0.75	0.107	0.70	0.106	0.69	0.096	0.65	0.105
June .	0.76	0.122	0.58	0.071	0.77	0.161	0.85	0.120	0.74	0.124
July .	0.21	0.061	0.42	0.043	0.62	0.083	0.17	0.030	0.39	0.060
Aug. .	0.68	0.084	0.74	0.082	0.79	0.105	0.31	0.056	0.63	0.084
Sept. .	0.42	0.048	0.77	0.083	0.22	0.023	0.59	0.062	0.52	0.056
Oct. .	0.70	0.093	0.73	0.070	0.56	0.065	0.58	0.085	0.63	0.077
Nov. .	0.43	0.078	0.74	0.110	0.39	0.059	0.37	0.053	0.50	0.077
Dec. .	0.39	0.072	0.51	0.073	0.61	0.055	0.45	0.058	0.50	0.060
Jan. .	0.53	0.060	0.54	0.103	0.63	0.070	0.58	0.089	0.50	0.080
Feb. .	0.04	0.005	0.28	0.036	0.53	0.063	0.64	0.118	0.44	0.064
Year .	0.50	0.070	0.52	0.074	0.57	0.075	0.55	0.078	0.56	0.074 ± 0.0030

TABLE 14.

Correlations and regressions of log. catch on minimum temperature from differences between successive days.

Period	Cor.	Reg.	Period	Cor.	Reg.
Four March . . .	0.37	0.069	Four Springs . . .	0.39	0.058
April . . .	0.32	0.042	Summers . . .	0.45	0.063
May . . .	0.45	0.074	Autumns . . .	0.41	0.056
June . . .	0.54	0.080	Winters . . .	0.38	0.056
July . . .	0.33	0.044			
August . . .	0.50	0.063	1933-34 . . .	0.38	0.054
September . . .	0.47	0.045	1934-35 . . .	0.39	0.053
October . . .	0.51	0.066	1935-36 . . .	0.41	0.062
November . . .	0.29	0.056	1936-37 (10 months) . . .	0.43	0.073
December . . .	0.33	0.060			
January . . .	0.39	0.063	All four years . . .	0.40	0.060
February . . .	0.44	0.079			± 0.0037

Table 14, on the other hand, shows the corresponding values for the four repetitions of each month, for each year, and for the four years together, calculated from the difference between successive days.

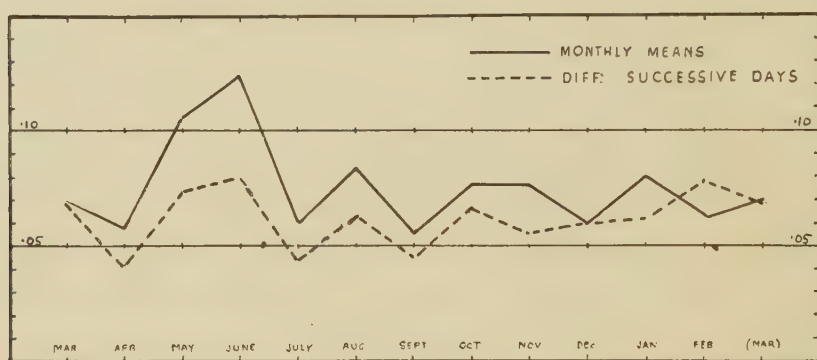
The average monthly regression calculated by each method is shown diagrammatically in fig. 9.

Two main differences are apparent. First that the regression by the method of differences between successive days is generally smaller than the value from

fixed monthly means. Secondly the values by the latter method for May and June are very much higher than the rest.

I think that both these differences are explained by the reasoning already put forward; namely, that the use of the fixed monthly mean causes the results of simultaneous trend to be included in the regression and correlation. In May and June both catch and temperature are increasing, and give a falsely high value to the regression, if this is looked upon only as a measure of "activity." In the autumn the difference is not so well marked, as the normal fall in the insect population is masked by the arrival in the trap of great numbers of winter gnats (*Trichocera*). This causes the average log. catch to remain high, and the average catch for November to be as high as that for October.

The mean regression of log. catch (of all insects) on minimum temperature for the whole period of four years, if calculated by the departure from fixed monthly means, is 0.074 ± 0.0030 per degree Fahrenheit, and the correlation 0.56 (on over 1400 values). This means that the catch is doubled (*i.e.* log.



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FIG. 9.—Regression of log. catch of all insects on minimum temperature. Mean of each month in all four years, calculated by departures from monthly means (solid line) and by differences between successive days (dotted line).

raised by 0.301) by an increase of temperature of 4° F. (2.2° C.); or, in the usual physical notation, $Q\ 10$ (the increase over 10° C.) = 21.5.

With the calculation based on differences between successive days the regression is 0.060 ± 0.0037 or the catch is doubled by 5° F. (2.8° C.); giving $Q\ 10 = 12.8$. If one is discussing "activity" only, this latter is almost certainly the more correct estimate.

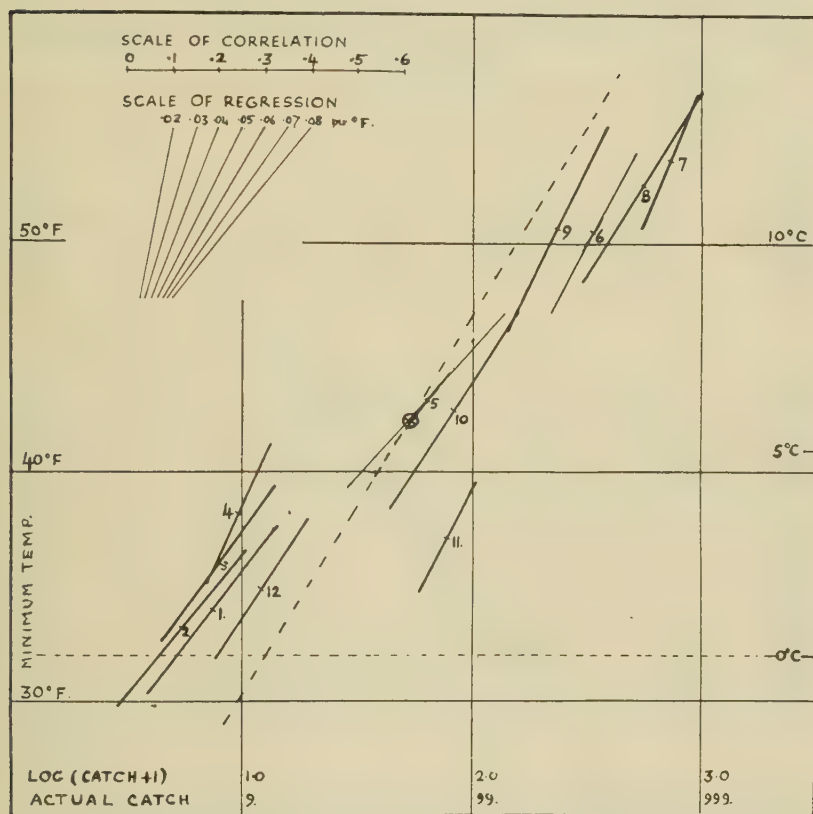
The values for the average regressions of catch on minimum temperature for each month in the year, based on the difference between successive days, are shown diagrammatically in fig. 10, together with the mean value for all four years as a dotted line. In this diagram an attempt has been made to indicate simultaneously both regression and correlation by making the length of the regression line proportional to the correlation according to a scale indicated on the diagram. Thus the longer the regression line on the figure the higher is the correlation.

Figs. 9 and 10 show quite definitely that there is practically no evidence of any seasonal change in regression value. The values for each month vary round the mean without any regular sequence.

As further evidence on this question an analysis of variance has been cal-

culated on the regressions (by method of differences) for the 48 months, showing the mean variance between months and between years as follows :—

	Degrees of freedom	Total variance	Mean variance
Total	47	38,887	827
Between years	3	2,316	772
Between months	11	7,080	644
Error	33	29,491	894



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FIG. 10.—Diagrammatic representation of regressions and correlations between log. total catch and minimum temperature in the different months of the year (each the average of 4 years) and the mean for the whole 48 months (dotted line). The length of the regression line represents the correlation on the given scale. The months of the year are represented by the numbers 1–12. Results calculated from differences between successive days.

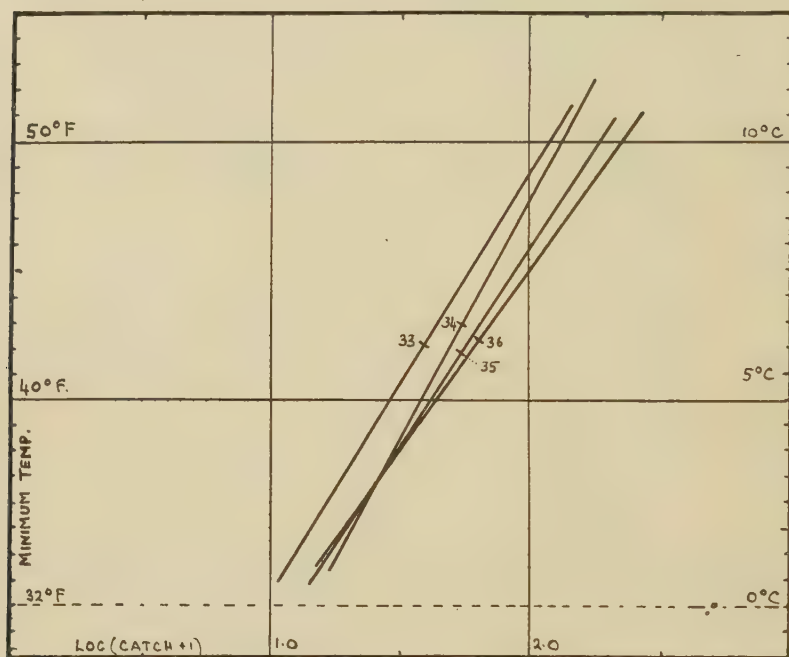
From this it will be seen that the mean variance between months and the mean variance between years are both less than the mean variance or the mean error, thus giving no evidence of either seasonal or annual variation.

If this interpretation is correct, and since the insect population caught in the trap is composed of quite different species in summer and winter, it would appear that the reaction of insect activity to minimum night temperature is not, on the average, specific to different insects, but is a fundamental property

of large groups and divisions of insects. In other words, the insects found at Rothamsted in the summer are reacting to minimum temperature changes in a very similar way to those found in winter although the species and often the families and orders are quite different. This will be referred to again later when the regressions for different groups of insects are discussed separately (see p. 263).

Fig. 11 shows diagrammatically the regression lines of the four successive years in which the trap was run, based on the difference between successive days. The similarity of the results is particularly striking.

To sum up, the method of calculating regressions and correlations from



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FIG. 11.—The regression lines for log. all insects and minimum temperature for each of the four years of trapping. Calculated from differences between successive days.

the differences between successive days appears to be the most reliable one, and when this is done it is found that the effect of the raising of the night minimum temperature by 1° F. is to raise the log. catch by 0.060 ± 0.0037 . Otherwise the catch is doubled by a rise in temperature of just under 5° F., or increased 13 times by a rise of 10° C.

The effect of minimum temperature on other than "Total Catch."

(a) *Insects in last period of night only.*

As the minimum temperature occurs usually just before dawn in the last period of the night, a calculation was made for the three months June to August 1933 to see if there was a closer relation between the minimum temperature

and the catch in the last period, than with the total catch for the whole night. The results are shown in Table 15.

It will be seen that there are slight differences within a single month; thus the correlations are lower in two months and the regression lower in one month for the 8th period only; but when the three months are combined there is no significant difference in either correlation or regression.

TABLE 15.

Correlations and regressions of log. catch in the last period of the night on minimum temperature.

1933	Correlation		Regression	
	8th period	Whole night	8th period	Whole night
June	0.54	0.73	0.109	0.123
July	0.34	0.29	0.069	0.068
August	0.65	0.68	0.083	0.084
Three months	0.53	0.56	0.088	0.091

(b) *Single-orders of insects.*

It has been shown above that when the regression on minimum temperature for all insects is calculated for each month of the year there is no significant difference between the values for the different months. But in the winter the catch is almost entirely Diptera while in July nearly 25% of the catch are Lepidoptera and other groups. Also the species of Diptera caught in the winter are different from those in the summer. It thus appeared that the regression might be typical of all insects and not vary from order to order or from species to species.

To test this in more detail, regressions on minimum temperature have been calculated for all Lepidoptera for the 3 summer months, June, July and August in the four years, and also for all Hemiptera for the two Augusts (1933 and 1935) in which over 1000 individuals were captured per month. In August of the other two years the numbers captured were too small to give reliable regressions.

The figures so obtained are shown in Table 16 with the corresponding

TABLE 16.

Correlations and regressions of the catch of Lepidoptera and of Diptera on minimum temperature.

	Cor.	Reg.	All insects in same period for comparison	
All Lepidoptera—				
3 June, 1933–35 ² . . .	0.60	0.0795	0.53	0.0799
4 July, 1933–36 . . .	0.36	0.0406	0.33	0.0442
4 August, 1933–36 . . .	0.55	0.046	0.49	0.0632
Total 11 summer months . . .	0.48	0.0516 ± 0.0052	0.44	0.0597 ± 0.0065
All Hemiptera—				
2 August, 1933 and 1935 . . .	0.61	0.083 ± 0.014	0.60	0.076

² In June 1936 the trap was not working regularly.

values for "all insects" for the same period. It will be seen that in no case are the differences significant. In the case of the Lepidoptera for the total of eleven months the difference between the two regressions is 0.0082 and the standard error of the difference 0.0084, so that this result could have been obtained by chance in 30% of trials.

In the Hemiptera for the two Augusts the difference is actually smaller and the error greater.

The question must finally be tested, by a study of single species but this problem will be dealt with in a later publication.

A calculation was also made of the correlations and regressions of the moths of the family NOCTUIDAE in the three summers (May to October) of the three years 1933-35. The figures for the NOCTUIDAE on which these are based had already been corrected for lunar effect by a method described in a previous paper (Williams 1936a). The results are shown in Table 17.

It will be seen that on the whole eighteen lunar months (526 days) the effect of one degree change in minimum temperature is to alter the log. catch by 0.051 ± 0.005 , which is quite comparable with the results obtained for all insects and for Lepidoptera only.

TABLE 17.

Correlations and regressions of the catch of NOCTUIDAE (corrected for lunar effect) and minimum temperature; from departures from monthly means.

Lunar month	1933		1934		1935	
	Cor.	Reg.	Cor.	Reg.	Cor.	Reg.
May	0.29	0.050	0.40	0.052	0.18	0.016
June	0.51	0.078	0.37	0.058	0.53	0.099
July	0.19	0.031	0.23	0.029	0.22	0.031
August	0.36	0.062	0.28	0.039	0.67	0.071
September	0.26	0.033	0.44	0.036	0.18	0.024
October	0.74	0.113	0.69	0.057	0.42	0.047
Six months	0.42	0.068	0.39	0.045	0.35	0.043
All 3 years			0.39	0.051 ± 0.005		

The error of the regressions on minimum temperature.

It has not been considered necessary to work out the standard error of the regression in all cases, but this has been done in several which are summarised in Table 18. Theoretically the error of the regression is inversely proportional to the square root of the number of observations. Thus a calculation based on twelve months should be twice as accurate as one based on only three months' observations. It will be seen how closely the calculated errors conform to this relation; and in the last column an approximate theoretical value has been given which can be used to find the length of the period of observation necessary to give any required accuracy.

Maximum temperature of the previous day.

Table 19 shows a summary of the correlations and regressions for total catch and maximum temperature calculated from the differences between successive days.

It must be remembered that this calculation, being a single regression, includes the positive or negative effect of any associated factors.

TABLE 18.

Errors of regressions on minimum temperatures in calculations for different numbers of months.

Period	Insects	Date	Error of regression	Approx. value by theory
One month	All insects	June 1933	0.021	} 0.024
	"	June 1934	0.024	
Two months	All Hemiptera	Aug. 1933 and 1935	0.014	} 0.014
Four months	All insects	Four Julys	0.012	
		Four Septembers	0.0077	} 0.012
Eleven months	All insects	Four Summers	0.0065	
	All Lepidoptera	"	0.0052	} 0.0072
Four years	All insects	"	0.0037	
	"	(Partial reg.)	0.0038	} 0.0035

It will be seen that the final regression for all four years is 0.042 (as compared with 0.060 for minimum temperature), which indicates that the catch is doubled following a rise of maximum temperature of about 7° F.

In the series of regressions of the individual months the lowest regression is in March (with a very low correlation) and the highest in December with a high correlation, but it is not really certain that the differences between these extremes are significant, particularly as the month following March gives a regression exactly equal to the average.

Spring gives a regression a little below the normal and winter a little above but again it is doubtful if their differences are significant.

It is curious to note that the year 1936-37 gives a very much higher regression than the other years and almost double that of 1933-34. The difference is mathematically significant on the error of regression. It will be seen from Table 2 (p. 231) that in 1933-34 the maximum temperatures were above the average of the four years in all the months from March to October. While in 1936-37 they were below the average except in May and December to February. This gives, therefore, a suggestion that maximum temperatures may have a greater importance in years of low maxima than in years of high maxima.

TABLE 19.

Correlations and regressions for log. catch on maximum temperature of the previous day; from differences between successive days.

Period	Cor.	Reg.	Period	Cor.	Reg.
Four March .	0.03	0.005	Four Springs .	0.21	0.032
April .	0.32	0.042	Summers .	0.34	0.043 ± 0.007
May .	0.28	0.038	Autumns .	0.20	0.044
June .	0.37	0.044	Winters .	0.25	0.050 ± 0.011
July .	0.30	0.039 ± 0.012			
August .	0.36	0.045	1933-34 .	0.19	0.030 ± 0.008
September .	0.29	0.043	1934-35 .	0.27	0.041
October .	0.28	0.063	1935-36 .	0.19	0.036
November .	0.08	0.022	1936-37 .	0.33	0.065 ± 0.011
December .	0.35	0.091			
January .	0.30	0.055 ± 0.016	All four years .	0.24	0.042 ± 0.005
February .	0.10	0.017			

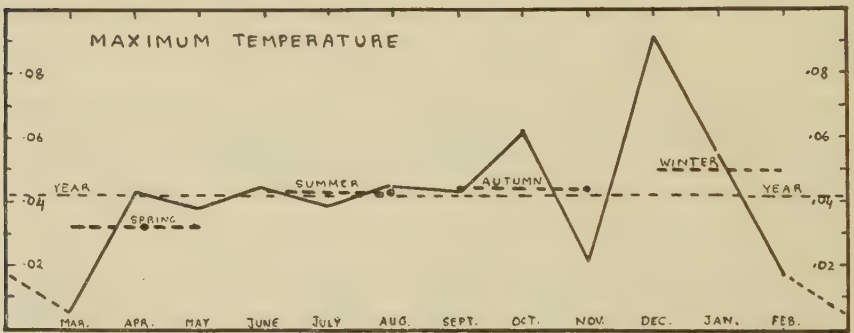
Fig. 12 shows the above results graphically for comparison with the similar figure (9) for the minimum temperature. It will be seen that the regressions are very even from April to September, but very irregular during the late autumn and winter months from October to March. There is no real evidence of regular seasonal change.

Analysis of variance of the regression for the 48 months shows, as in the case of the minimum temperature, that the differences between months and between years are both smaller than the mean error.

Grass minimum temperature.

Grass minimum temperature is closely correlated with the screen minimum temperature, but is considerably more variable. For example, the total variance (sum of squares) for the six months (178 days) June, July and August in 1933 and 1934 is 7252 for the grass minimum and only 3471 for the screen minimum.

Table 20 shows the regressions and correlations calculated by the method



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FIG. 12.—Sequence of mean monthly regressions of log. total catch on the maximum temperature of the previous day, calculated from the difference between successive days.

of differences between successive days for each of these six months, and also the total for each summer and the two summers combined. It will be seen that the

TABLE 20.

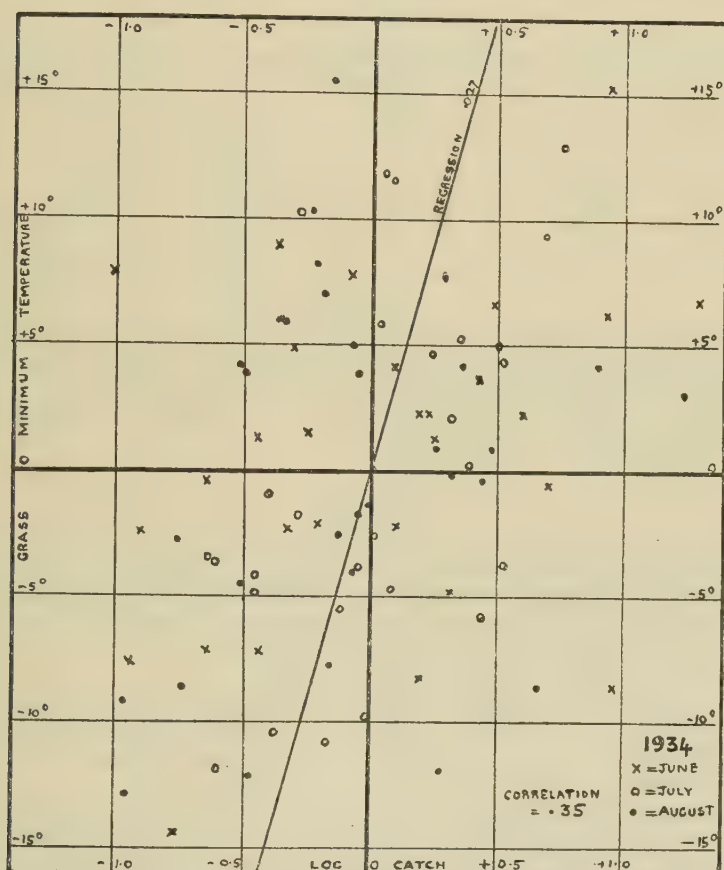
Correlations and regressions for log. catch and the grass minimum temperature, from differences between successive days.

	1933		1934	
	Cor.	Reg.	Cor.	Reg.
June	0.64	0.074	0.35	0.0333
July	—0.04	—0.003	0.50	0.0278
August	0.41	0.036	0.26	0.0203
All 3 months	0.28	0.0339	0.35	0.0268
All six months		Cor.		Reg.
Figures of screen min. for comparison		0.35		0.0299
		0.48		0.0583

final correlation is 0.35 and that each degree change of grass minimum temperature alters the log. catch by 0.030. Thus a rise of approximately 10° F. will double the catch.

In the same table it is shown that the corresponding figures for the same period for the screen minimum are 0.48 and 0.058; both considerably higher.

Analysis of variance shows a mean daily variance of 0.2921 for the trap for



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FIG. 13.—Scatter diagram and regression lines for the relation between the log. total catch and the grass minimum temperature for June, July and August 1934 from difference between successive days.

the six months, of which only 0.0337 (12%) is explained by the regression on the grass minimum and 0.0651 (22%) by the regression on screen minimum. The screen minimum therefore is a better indication of the catch variation than is the grass minimum.

Fig. 13 shows as a scatter diagram the catch and grass minimum on all nights in the summer of 1934, expressed as differences between successive days; and also the regression line through these points.

Daily range of temperature.

The discussion on p. 246 on the differences in daily range between nights of high and low catch made it unlikely that any significant relation would be found. However, to bring the data in a line with the other analyses, regressions and correlations have been calculated for the three summer months in 1933, by the method of differences between successive days, and are shown in Table 21.

TABLE 21.

The relation of log. catch to daily range of temperatures from differences between successive days.

	Cor.	Reg.
1933 June	-0.32	-0.039
July	+0.05	+0.003
August	+0.10	+0.011
All three months	-0.05	-0.0039

The results show that in one month the relation was negative and in the other two months positive, and that the average of the three months is a small negative effect which is well below the limits of significance. The scatter diagram for all these months is given in fig. 14, and shows graphically the absence of any definite relationship.

Humidity.

Owing to the close manner in which air humidity is tied up with temperature very little analysis was made on the direct effect of this factor on catch.

On p. 249 has already been given a comparison of the relative humidities on nights of high and of low catch and later there will be given simultaneous analyses of humidity and 9 p.m. temperatures (see p. 291); and humidity wind and maximum and minimum temperature (294).

Table 22, however, shows the simple correlation and regression of 9 p.m. relative humidity on total catch in the year 1933-34. The other years cannot be added as the 9 p.m. observations were discontinued and the recording instrument was not sufficiently accurate.

It will be seen that spring, autumn and winter all give positive correlations and regressions, of which the autumn values are the highest. The summer value is a non-significant negative one. For the whole year the regression is $+0.0078 \pm 0.0037$, which is just significantly positive at the 5% level but not at the 2%.

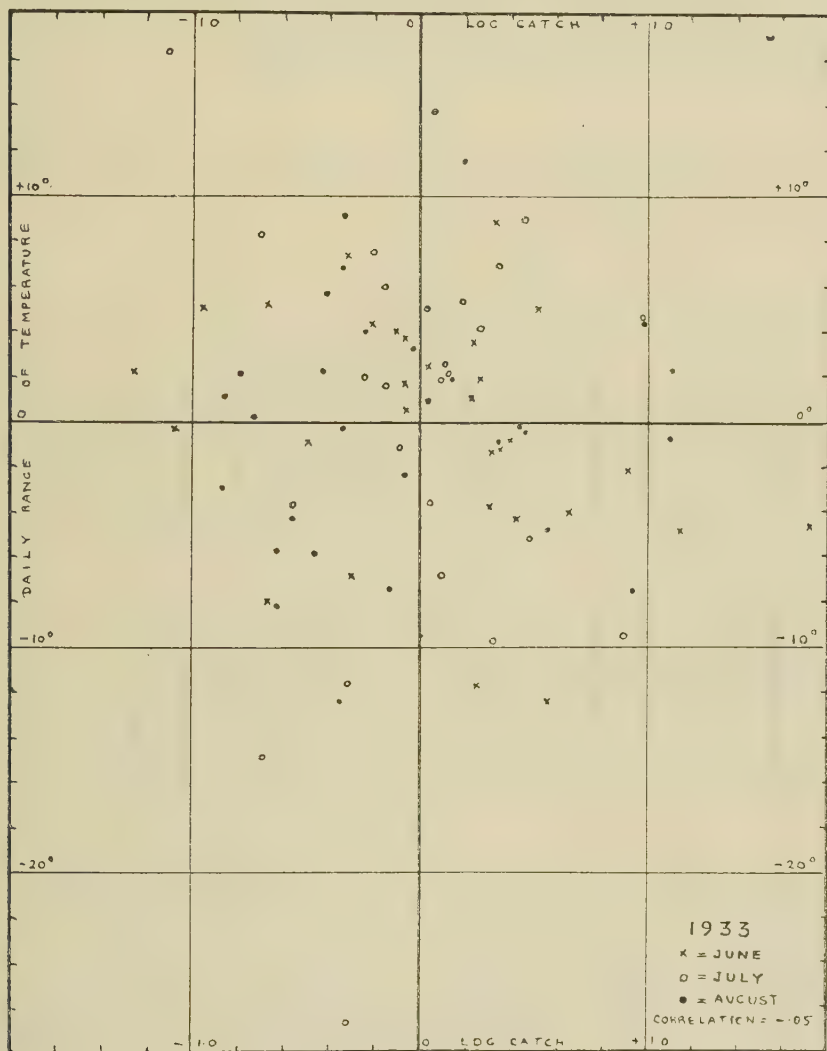
TABLE 22.

Correlations and regressions of insects on relative humidity at 9 p.m.; from differences between successive days, 1933-34.

	Cor.	Reg.
Spring (March-May)	+0.14	+0.0093
Summer (June-August)	-0.03	-0.0013
Autumn (September-November)	+0.22	+0.0193
Winter (December-February)	+0.16	+0.0138
All year	+0.11	+0.0078 $\pm$ 0.0037

Rain.

Owing to the evidence already produced (p. 247) that there is practically no difference between the incidence of night rain between nights of high and low catch, little statistical analysis has been done.



14

FIG. 14.—Scatter diagram of relation between log. total catch and daily range of temperature for June to August 1933, showing the absence of any correlation between the two.

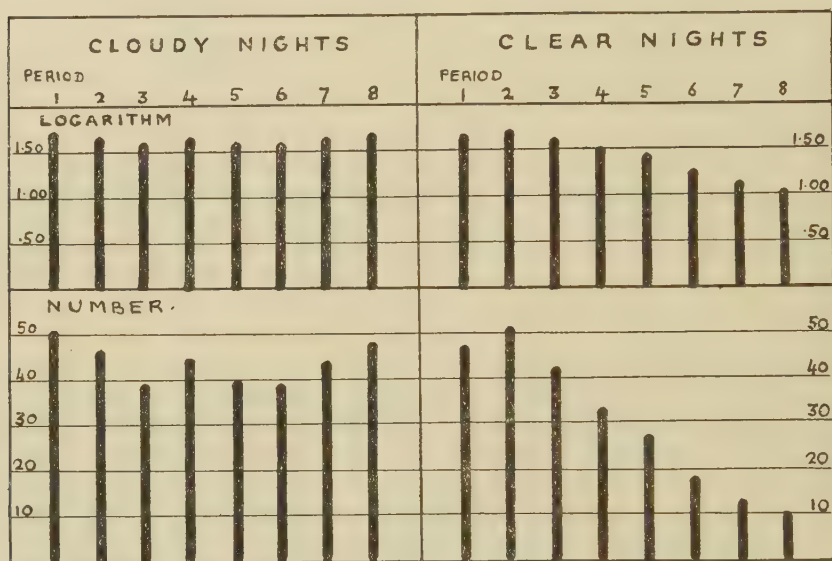
However, a study was made of the 66 nights in 1933, on which rain fell during the period 6 p.m. to 6 a.m., and this showed that these nights had a log. catch 0.02 above normal, and that the regression was $+0.017$ per 0.1 inch of rain. On further inspection, however, it was found that the rainy nights

had an average minimum temperature 1.3° F. above normal, which is in itself more than sufficient to account for the slight increase in catch.

On the other hand, an analysis of the effect of day rain (in the period 6 a.m. to 6 p.m.) over the same period showed that the 71 nights following day rain had an average log. catch $+0.168$ below normal, and that the regression was -0.068 per 0.1 inch of rain. In this case, however, it is found that the average temperature of the nights is 0.7° F. below normal, so part at least of this effect of day rain may be caused by the lowered temperature.

Cloud.

No direct calculations have been made on the effect of cloud on the total number of insects captured during the night as this effect is mostly indirect.



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FIG. 15.—Distribution during the eight periods of the night of all insects on clear and on cloudy nights. Given first on logarithmic basis and then as actual number.

The amount of cloud affects night temperature, humidity and moonlight, and through them the catch.

In the course of the work, however, a comparison has been made of the distribution of the insects in the eight periods of the night into which the catch is divided (see Williams 1939: 119) on the 46 cloudy nights and the 52 clear nights in the summer of 1935, from May to October inclusive.

The figures are shown in Table 23 and diagrammatically in fig. 15. It will be seen how much later the night activity continues when the sky is covered with clouds. In fact the number of insects at dawn on the cloudy nights is almost as great as at dusk, whereas on the clear nights the catches at dawn are only about one-fifth of those at dusk.

Other details on the distribution of insects will be found in the first part of this paper (Williams 1939).

The combined effect of cloud and moon is discussed on p. 274.

TABLE 23.

Difference between night distribution of insects on clear and cloudy nights during the summer of 1935.

	Period of night							
	1	2	3	4	5	6	7	8
As log. ($n + 1$):								
Clear	1.68	1.72	1.63	1.53	1.45	1.27	1.13	1.06
Cloudy	1.72	1.68	1.60	1.66	1.61	1.60	1.65	1.69
As number (antilog. of above -1):								
Clear	47	51	42	33	27	18	13	10
Cloudy	51	47	39	45	40	39	44	48

Fog.

Fog is of course only an extreme case of high humidity, super-saturation or a negative "saturation deficiency." It has, however, a quite new biological effect owing to its interference with visibility.

In general in the Rothamsted district fog occurs during the late autumn and winter months, especially in November and December, and on nights when the temperature is below normal. The catches on such nights are usually very poor.

In 1933, however, on the night of the 28th September there was a dense fog, starting about 4 p.m. and lasting throughout the night and the early part of the following day; visibility was at times not more than a few yards. The catches, particularly in the family NOCTUIDAE, on that night were so unusual that they seem worthy of special discussion.

The maximum temperature on the 28th September was 67.3° F. (exactly normal for the month but a little above the average for the end of the month). The minimum temperature was 45.4° F. (6.1° F. below the month's normal) and the grass minimum 41.4° F. (5.1° F. below the month's normal). Two traps were working on that night: one, trap A, in its usual position; the other, trap B, on the roof of the Entomological Laboratory at a height of about 35 feet. Both had the same light intensity (see Williams 1939: 93 for general discussion of the catches in this trap).

The capture of all insects for trap A was 148, of which 37 were Lepidoptera and 100 Diptera. The mean catch per night for the month in this trap was 221 so that the foggy night gave a total below the average. The Lepidoptera, however, included 36 NOCTUIDAE of 5 species, which was the second highest total of this family for the month and far above the month's average of 12 NOCTUIDAE per night. The distribution of the NOCTUIDAE in the successive periods of the night was 0:0:8:9:4:13:2:0.

In trap B only the Lepidoptera were recorded, and these included 104 NOCTUIDAE of 14 species, again the second highest total of the month and more species than on any other night in the month.

The actual species captured are shown in Table 24.

All the species in trap B, except *A. lychnidis* and *A. lunosa*, came in larger numbers than on any other day in the month. Twelve *P. meticulosa* were captured in trap B out of a total of only 37 captured in both traps in all four years.

The most remarkable case is, however, that of *A. circellaris*. Twenty-two

TABLE 24.

Captures of NOCTUIDAE on night of heavy fog in September 1933.

	Trap A	Trap B
<i>T. pronuba</i> (L.)	—	2
<i>A. ypsilon</i> (Rott.)	—	5
<i>A. litura</i> (L.)	—	4
<i>P. flavicincta</i> (S.V.)	—	5
<i>A. lychnidis</i> (Rbr.)	30	34
<i>M. gilvago</i> (Esp.)	3	4
<i>A. lunosa</i> (Hw.)	1	2
<i>P. gamma</i> (L.)	—	2
<i>A. luteolata</i> (Bkh.)	—	4
<i>A. sarucia</i> (Hüb.)	—	3
<i>P. meticulosa</i> (L.)	—	12
<i>E. satellitia</i> (L.)	—	2
<i>A. circellaris</i> (Hufn.)	1	22
<i>A. segetum</i> (Schiff.)	—	3
<i>N. c-nigrum</i> (L.)	1	—
Total	36	104

of this species were captured in trap B and one in trap A. Throughout the whole of the remaining nights in which either of the two traps were used, only one other individual was captured in trap A (in 1934) and four others in trap B (2 in 1933 and 2 in 1934); so that out of a total catch of 28 in both traps in four years (trap B not in continuous use) 23 came on this one night of thick fog.

It is difficult to suggest an explanation, particularly as no other fog occurred so early in the autumn in the other three years. It is, however, possible that some of the insects found the broad area of illuminated fog more attractive than the bright point of light; or again it is possible that the fog did not extend very high above the ground and that many moths were flying above it and were attracted to the upper light. This would not, however, explain the catch of NOCTUIDAE in the lower trap (only 3 feet 6 inches above the ground), which was larger than normal, though not so large as that in the upper trap.

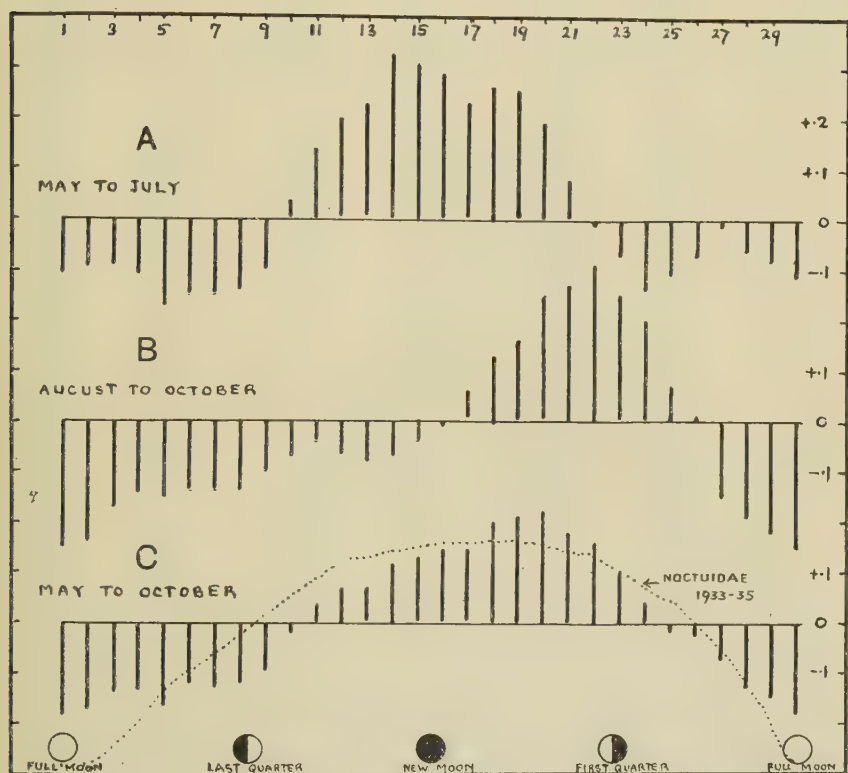
Moonlight.

In a previous paper (Williams 1936a) I have discussed in some detail the effect of moonlight on the catches in the trap, particularly on the family NOCTUIDAE of the Lepidoptera. Tables and figures were then given showing the average departure of the log. catch from the mean on each successive day of the lunar period in the summer months of 1933–35.

It is now possible to add another year (1936) to the analysis, but it has been considered more interesting to deal this time with "all insects" instead of with the NOCTUIDAE only. The results for all four years for the six summer months are shown in Table 25 and also, smoothed to a 5-day running mean in fig. 16, C and as actual numbers (with the mean catch 100) in fig. 17. It will be seen that the maximum negative departure in the log on the smoothed curve is — 0.18 on the day of full moon (equivalent to a catch 34% below normal) and the maximum positive departure is + 0.22 a few days after new moon (equivalent to a catch 66% above normal). The dotted line superimposed on the histogram shows the results previously obtained for the NOCTUIDAE

in the years 1933-35. The insects as a whole show a less extreme negative departure at full moon than the NOCTUIDAE, but a higher positive departure in the first quarter. The range in percentage of the mean is, as seen in fig. 17, from 66% at full moon to 166% during the first quarter.

It will be noted that the curve is slightly asymmetrical. It was suggested in the previous paper (Williams 1936a) that this was due to certain asymmetries in the time of rising and setting of the moon. These are different before and



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FIG. 16.—Diagram showing the average log. departure from the mean of the catches of all insects on the successive days of the lunar month. Each shows the average of the six summer months in all four years and they are smoothed to 5-day running means. The dotted line in the lower figure shows the results previously obtained for the family NOCTUIDAE for the three years 1933-35.

after the middle of June, and it was shown that if the results obtained for the NOCTUIDAE are calculated in two portions, one before and one after the middle of June, they show opposite asymmetries as expected by the theory. The asymmetry of the full curve May to October is thus merely due to the fact that it contains a longer period with one asymmetry than the other.

An attempt has been made to demonstrate the truth of this relationship from the data now available for all insects. This has been divided into two series: the first including May, June and July and the second August, September and October (Table 25 and fig. 16, A and B). If the reasoning is correct the

TABLE 25.

Departure of log. catch of all insects from the normal on successive days in the lunar months in May to October of the four years.

Day of lunar month	May to July		August to October		May to October	
	Actual	5-d. mean	Actual	5-d. mean	Actual	5-d. mean
(Full) 1	-0.21	-0.11	-0.31	-0.25	-0.26	-0.18
2	-0.11	-0.10	-0.26	-0.24	-0.17	-0.17
3	-0.16	-0.09	-0.32	-0.17	-0.24	-0.13
4	+0.08	-0.11	-0.02	-0.14	+0.02	-0.13
5	-0.07	-0.17	+0.05	-0.15	±0	-0.16
6	-0.31	-0.15	-0.17	-0.14	-0.24	-0.12
7	-0.39	-0.15	-0.31	-0.14	-0.35	-0.13
8	-0.07	-0.14	-0.23	-0.14	-0.15	-0.12
9	+0.09	-0.10	-0.06	-0.10	+0.01	-0.10
10	-0.03	+0.04	+0.05	-0.07	+0.01	-0.02
11	-0.09	+0.14	+0.06	-0.04	-0.01	+0.04
12	+0.29	+0.20	-0.17	-0.06	+0.05	+0.07
13	+0.43	+0.23	-0.10	-0.08	+0.15	+0.07
14	+0.40	+0.33	-0.15	-0.07	+0.13	+0.12
(New) 15	+0.14	+0.31	-0.05	-0.04	+0.05	+0.13
16	+0.38	+0.29	+0.10	+0.01	+0.23	+0.15
17	+0.21	+0.23	-0.02	+0.07	+0.10	+0.15
18	+0.33	+0.27	+0.18	+0.13	+0.25	+0.20
19	+0.09	+0.26	+0.12	+0.16	+0.11	+0.21
20	+0.34	+0.19	+0.29	+0.25	+0.31	+0.22
21	+0.31	+0.08	+0.21	+0.27	+0.26	+0.18
22	-0.14	-0.01	+0.46	+0.31	+0.17	+0.16
23	-0.21	-0.07	+0.25	+0.25	+0.03	+0.10
24	-0.37	-0.14	+0.36	+0.20	+0.01	+0.04
25	+0.05	-0.11	-0.01	+0.07	+0.02	-0.02
26	-0.02	-0.07	-0.08	+0.01	-0.05	-0.03
27	-0.01	-0.01	-0.18	-0.15	-0.10	-0.07
28	+0.02	-0.06	-0.06	-0.19	-0.02	-0.13
29	-0.10	-0.08	-0.30	-0.22	-0.20	-0.15

first portion should contain an equal period on either side of the middle of June and so the two asymmetries should balance; the portion for August to October should show an asymmetry much more definite than the six months curve.

It will be seen that both these results have been obtained, thus leaving practically no doubt that the asymmetry of the curve is due to the causes previously suggested.

The variance due to the lunar influences has been calculated from the smoothed curves for the period May-July and for the period August-October for all insects. The total variance per lunar month is 0.0996 in the first case and 0.0916 in the second or a mean variance of about 0.0033 per day.

Another method of analysis of the lunar effect, this time also introducing the modifying effect of cloud, consists of dividing the days into nine categories according to the interrelation of two sets of three factors.

(1) According to the moon :—

- (a) nights in week of full moon;
- (b) nights in week of intermediate moon (first and last quarter);
- (c) nights in week of new moon.

(2) According to night cloud :—

- (a) nights with less than 10% cloud (clear);
- (b) nights with 10–90% cloud (intermediate);
- (c) nights with over 90% cloud (cloudy).

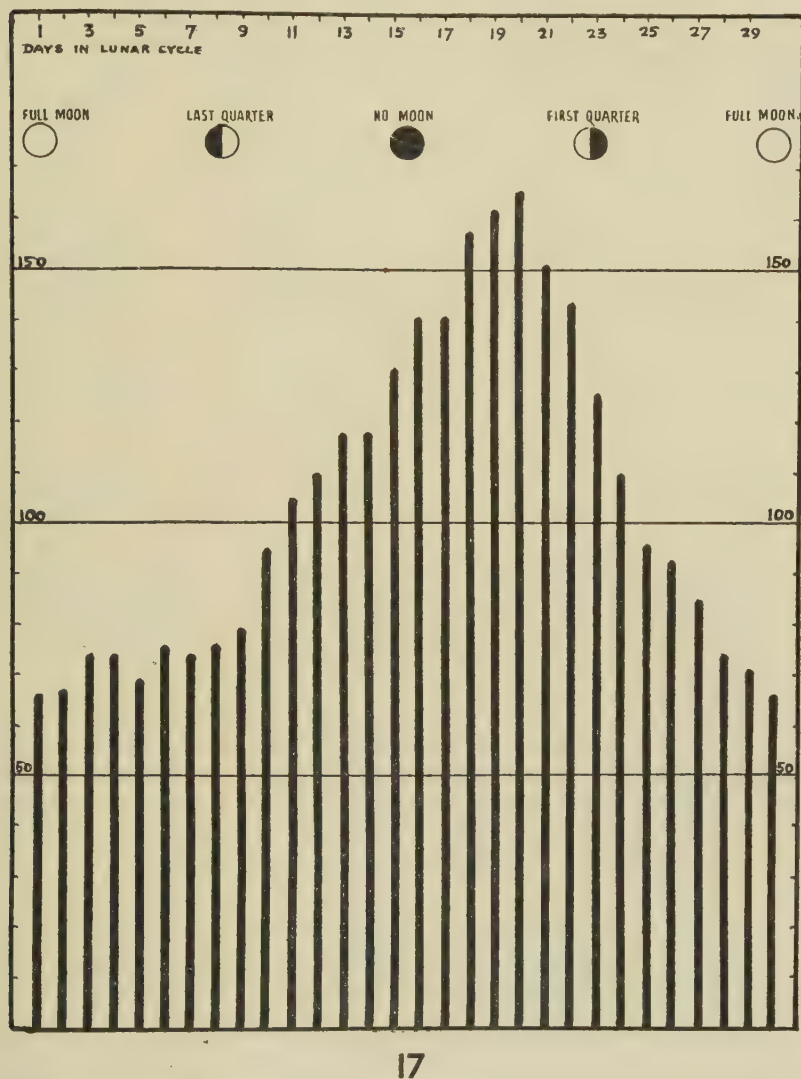


FIG. 17.—Mean number of insects caught on successive days in the lunar cycle in the six summer months (May to October) in the four years. Numbers calculated by reconversion from mean logarithms.

The mean log. departure for the nights in each of the nine categories is calculated from the catches on the nights in each group, and this figure is converted to a percentage mean catch.

Table 26, A and B, shows the results previously obtained by this method for the NOCTUIDAE and for all insects during 1933–35 (Williams 1936a). Table

26, C shows the number of nights which occurred in each category in the four summers of 1933-36. There is a total of 703 nights with a minimum of 43 in any one group (the "no-moon; cloudy").

One of the remarkable differences between the results previously obtained for the "NOCTUIDAE" and "all insects" was the very high numbers obtained for the latter in the "no-moon; cloudy" group, or under optimum conditions of flight. The figure for the NOCTUIDAE under these conditions is 184% of the mean, while for "all insects" it is 381%.

TABLE 26.

Percentage catch of all insects under various conditions of moon and night cloud.												
A					B				C			
NOCTUIDAE, 1933-35					All insects, 1933-35				No. of days, 1933-36			
	Clear	Int.	Cloudy		Clear	Int.	Cloudy		Clear	Int.	Cloudy	
Full moon .	42	49	95	54	63	69	115	74	56	77	45	178
Int. moon .	92	133	141	120	70	105	129	97	103	164	94	361
No moon .	128	144	184	146	81	138	381	151	52	69	43	164
	80	110	140		74	100	166		211	310	182	
D					E				F			
All insects, 1933					All insects, 1934				All insects, 1935			
Full moon .	145	74	148	107	47	87	83	64	24	56	123	57
Int. moon .	68	66	120	78	78	135	120	111	71	115	155	104
No moon .	93	107	309	117	87	132	323	144	68	218	468	194
	88	77	144		67	122	147		57	92	203	
G					H							
All insects, 1936					All insects, 1933-36							
Full moon .	38	48	234	77	57	62	148	76				
Int. moon .	66	105	151	92	71	105	135	100				
No moon .	162	148	186	161	93	141	323	151				
	71	90	181		71	97	170					

Table 26, D, E, F, and G, shows the values obtained for all insects in each of the four years separately, including 1936 not previously considered. It will be seen that the high activity in "no-moon; cloudy" occurs very definitely in each of the first three years but is not well marked in 1936. The new combined total for the four years (Table 26, H) still shows very considerable activity in this section.

If cloud is neglected the average % catch of all insects over the four years is 76 on nights in the week of full moon, 100 on intermediate nights and 151 on nights of the week of no moon. This difference has been shown to be independent of temperature.

If the phase of the moon is neglected the catch averages 71% on clear nights, 97% on intermediate nights and 170 on cloudy nights. This difference, however, is associated with a temperature difference of about 4° F. between the warmer cloudy and the cooler clear nights.

TABLE 27.

Percentage catch of certain families of insects under various conditions of moon and night cloud.

GEOMETRIDAE				PSYCHODIDAE				CECIDOMYIDAE				CERATOPOGONINAE			
1933				1933				1933				1933			
104	122	118	112	90	137	129	110	141	93	158	129	96	129	100	107
82	92	119	65	49	88	86	72	66	104	89	85	69	93	122	92
115	93	195	119	109	75	179	105	93	82	174	103	152	103	246	144
95	97	132		70	91	109		90	95	116		90	102	138	
1934				1934				1934				1934			
55	78	54	62	55	58	51	55	62	58	49	58	54	124	79	79
111	126	93	115	96	123	91	108	107	138	113	123	95	112	120	110
110	150	306	162	97	135	437	162	116	141	389	170	92	119	398	150
90	119	126		81	108	140		92	116	145		79	116	186	
1933 and 1934				1933 and 1934				1933 and 1934				1933 and 1934			
66	93	76	76	70	84	84	77	92	70	92	84	71	125	89	90
92	113	113	107	68	104	86	86	82	121	95	101	78	104	121	98
117	120	296	153	101	97	287	131	104	104	256	131	116	108	315	147
89	112	141		75	99	120		90	104	125		84	109	154	

Data are also available for several other groups of insects for 1933 and 1934 and this is shown summarised in Table 27 for the families GEOMETRIDAE, PSYCHODIDAE, CECIDOMYIDAE and CERATOPOGONINAE. It will be noted that in all four groups in 1933 the "full moon" figures are rather larger than the intermediate moon figures and in two families were actually larger than the "no moon" figures. This is due to the fact that in 1933 in five out of the six summer lunar periods heat waves occurred about full moon, making this period distinctly warmer than at no moon. Somewhat the reverse happened in 1934 so that the combined totals for 1933 and 1934 eliminated most of this source of error.

It will be seen that higher catches occur in the "no-moon; cloudy" section in all four groups than in the NOCTUIDAE previously dealt with, and also higher catches in the "full moon; clear."

The explanation previously suggested was that the NOCTUIDAE are more generally tolerant of conditions of flight but dislike the worst conditions of full moon and little or no cloud: the other insects are generally somewhat intolerant of unfavourable conditions but develop great activity under the optimum conditions of "no moon and full cloud." This explanation appears to hold for the present results also.

The GEOMETRIDAE are a family of Lepidoptera. The PSYCHODIDAE and CECIDOMYIDAE are families of Diptera. The former particularly came in in very large numbers, and made up about 70,000 of the 73,000 insects caught on the night of the highest catch in the four years. The CERATOPOGONINAE is a sub-family of the family CHIRONOMIDAE and includes a number of small blood-sucking species mostly with mottled wings. On the data available the CERATOPOGONINAE show the highest increase under conditions of "no moon and cloud."

Wind.

Wind records are taken continuously at Rothamsted by means of a Dines Anemograph, which records simultaneously the direction and force of the wind. The vane is at a height of about 70 feet above the ground on one of the main buildings of the Experimental Station.

An examination of a large number of charts shows that the calmest time of the day is during the hours of darkness (when the trap is working) and particularly after midnight.

For purposes of analysis the wind conditions during the night were divided into six artificial groups shown in Table 28.

TABLE 28.

Definition of six wind groups adopted for analysis.

Group	Wind	Approximate Beaufort scale
1	Dead calm, no trace of movement of pen of recording instrument	0
2	Almost calm, slight pen movements indicating velocities seldom over 2 m.p.h.	Just above 1
3	Velocities frequently 2-5 m.p.h.	Distinctly less than 2
4	Velocities frequently 5-10 m.p.h.	Rather less than 3
5	Velocities frequently 10-20 m.p.h.	4
6	Velocities frequently over 20 m.p.h.	5 and over

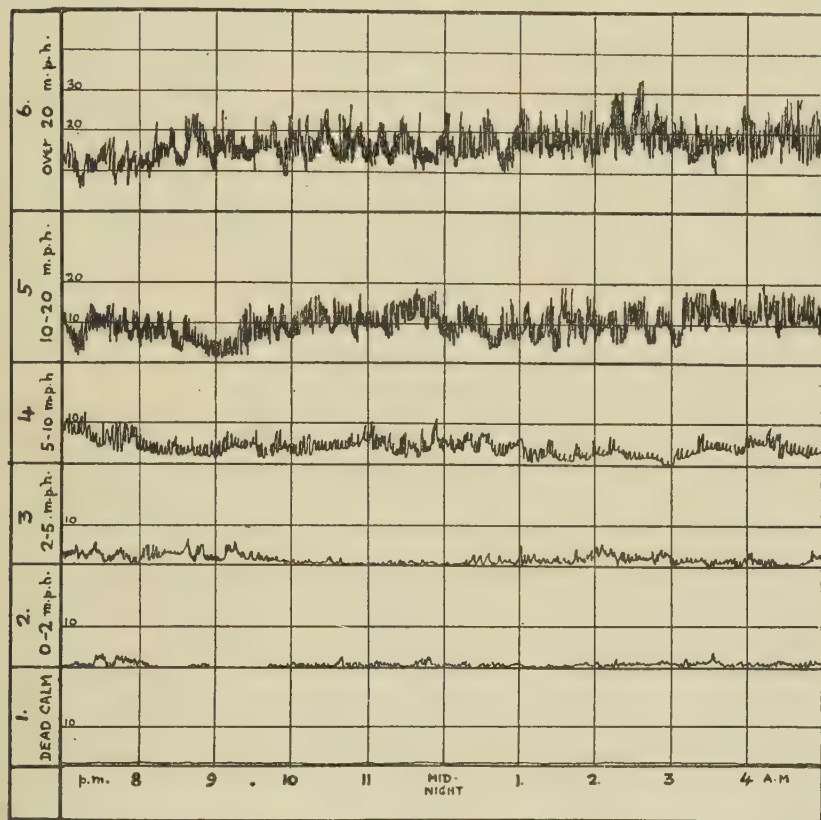
TABLE 29.

Frequency of occurrence of different wind groups in different months of the year, and mean wind value for each month.

Wind group	Frequency of different wind intensities						Mean wind group
	1	2	3	4	5	6	
March (4 years)	39	14	14	29	16	4	2.8
April	28	10	26	26	23	3	3.1
May	30	20	14	15	26	1	2.8
Spring total (338 nights) .	97	44	54	70	65	8	
June	52	14	12	15	12	2	2.3
July	52	23	15	15	15	1	2.2
August	65	17	15	13	9	0	2.0
Summer total (347 nights) .	169	54	42	43	36	3	
September	38	22	13	28	16	3	2.8
October	22	17	10	28	34	12	3.6
November	25	15	23	22	28	6	3.3
Autumn total (362 nights) .	85	54	46	78	78	21	
December	21	19	13	24	40	5	3.5
January	20	18	12	25	33	12	3.5
February	23	12	12	20	32	8	3.5
Winter total (349 nights) .	64	49	37	69	105	25	
Four years total (1396 nights)	415	201	179	260	284	57	3.0

Typical charts from the anemograph for nights in each class are shown in fig. 18. These groups do not correspond exactly to the Beaufort scale, as I was attempting to get a scale which increased its range more or less geometrically in each successive group; the approximate Beaufort number is shown in the last column of the table.

Most of the nights were relatively easy to classify, but a number were difficult and a few impossible. The latter were omitted from the calculations. The chief difficulty was due to rapid change in wind conditions during a single



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FIG. 18.—Typical wind charts from Dines anemograph for nights in the six classes into which the wind conditions have been divided.

night. In making a decision conditions before midnight (when the greatest number of insects are flying) were generally allowed to count more than conditions after midnight, and the wind was rather over- than under-estimated in order that the wind effect would not be exaggerated. In some doubtful cases the night distribution of the insects on that night was also taken into consideration.

Table 29 shows the frequency of occurrence of the nights in each class in each month of the year, together with seasonal and annual summaries. It will be seen that the annual distribution curve has two peaks, one at "calm" and one with winds 10-20 m.p.h. (Group 5). Of the total of 1396 nights, 415

TABLE 30.

Log. catch departure from normal, and minimum temperature departure from normal, in the different wind groups in each month of the year. Based on 4 years data.

Wind group	Catch log. departure						Temperature departure					
	1	2	3	4	5	6	1	2	3	4	5	6
March .	+0.26	+0.06	-0.06	-0.07	-0.33	-0.53	-1.4	-0.3	+0.3	+0.7	+1.3	-0.3
April .	+0.28	+0.29	+0.10	-0.13	-0.24	-0.93	-2.1	-1.6	-1.4	+1.3	+1.1	+7.5
May .	+0.17	+0.08	-0.11	-0.28	-0.13	-1.17	-0.5	-0.2	+1.5	-0.5	+0.6	-3.6
Spring .	+0.24	+0.12	+0.00	-0.14	-0.22	-0.76	-1.3	-0.5	+0.4	+0.7	+1.0	+2.2
June .	+0.36	-0.37	-0.14	-0.10	-0.80	-1.02	+1.2	-2.0	-1.0	-0.1	-0.5	+0.9
July .	+0.24	+0.06	+0.12	-0.38	-0.62	-0.84	-0.9	+0.5	-0.4	+1.5	+1.4	-0.8
August .	+0.15	-0.08	+0.04	-0.31	-0.54	—	-0.4	-1.0	+1.4	-0.2	+1.5	—
Summer .	+0.24	-0.10	+0.02	-0.26	-0.60	-0.96	-0.0	-0.6	+0.0	+0.4	+0.8	+0.3
September .	+0.02	+0.07	+0.10	+0.05	-0.21	-0.75	-1.6	-0.5	+1.0	+1.4	+1.0	+0.2
October .	+0.01	-0.08	+0.36	+0.19	-0.08	-0.40	-1.4	-3.2	+1.4	+0.6	+0.5	+2.5
November .	+0.05	-0.11	+0.21	+0.11	-0.17	-0.52	-2.1	-3.6	-1.4	+2.1	+1.5	+4.2
Autumn .	+0.03	-0.03	+0.22	+0.12	-0.14	-0.48	-1.7	-2.3	-0.0	+1.3	+1.0	+2.7
December .	+0.23	-0.06	-0.01	+0.08	-0.04	-0.52	-2.3	-4.0	-3.3	+1.0	+2.8	-0.6
January .	-0.76	+0.17	+0.23	+0.14	-0.09	-0.40	-5.0	-1.8	+1.5	+0.3	+2.0	+0.9
February .	+0.01	+0.75	-0.11	-0.17	+0.01	-0.26	-1.8	0.9	-0.8	-0.0	+1.2	+0.4
Winter .	+0.06	+0.19	+0.06	+0.03	-0.03	-0.34	-3.0	-1.6	-0.9	+0.5	+2.1	+0.5
Whole year	+0.17	+0.03	+0.07	-0.04	-0.18	-0.48	-1.1	-1.3	-0.1	+0.8	+1.3	+1.5

(30%) were calm and 57 (4%) had winds of over 20 m.p.h. Of the 415 calm nights 254 (61%) occurred in the summer and autumn; while of the 57 stormy nights 46 (80%) occurred in the autumn and winter months.

The method of analysis consisted in placing in the correct wind group the value of the catch (log. departure from 29-day mean) for each of the nights and finding the average catch departure for all nights in that category. The values for each month (4 repetitions in 4 years) have been kept separately.

Table 30 shows the results of this analysis for all insects. Thus from the top line one sees that in all the four months of March the log. catch was 0.26 above normal on calm days, 0.06 above normal with wind group 2 (0-2 m.p.h.), 0.06 below normal with wind 3, 0.07 below normal with wind 4, 0.33 below normal with wind 5 and 0.53 below normal for wind group 6.

The final values for the whole period calculated from nearly 1400 nights are shown in the lowest line of the table, and also graphically in fig. 19, A and B. The general result is that on calm nights the log. catch is 0.17 above normal and on stormy nights 0.48 below or an average change of 0.13 per group. The values of each group expressed as actual numbers with the catch on calm nights as 100 are as follows:—

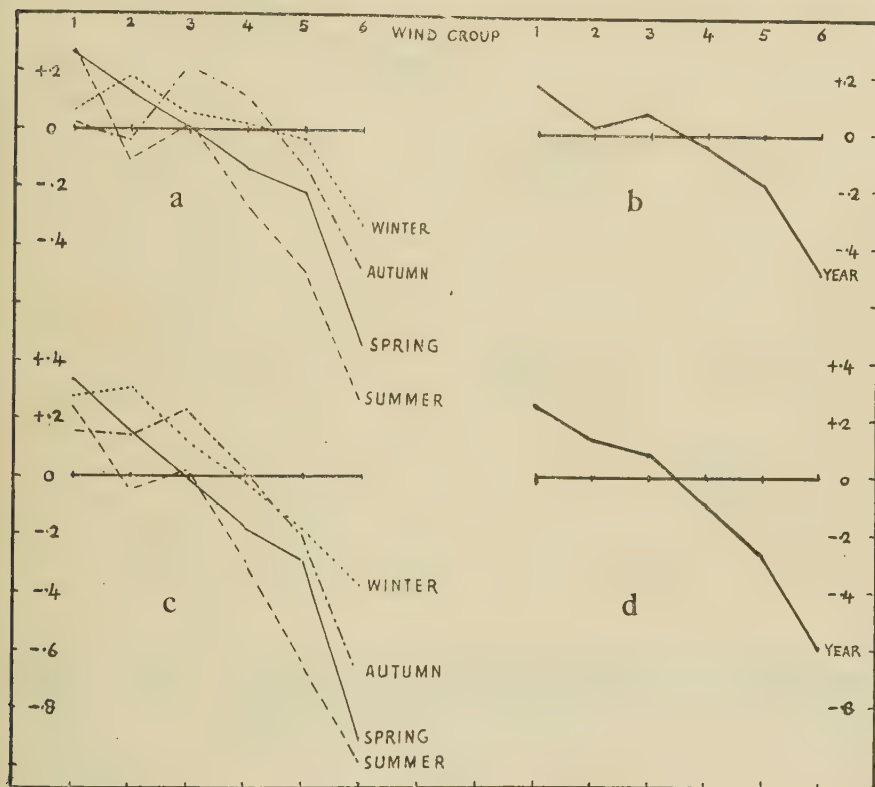
Wind group	.	.	1	2	3	4	5	6
Mean catch	.	.	100	73	81	63	46	22

It will be seen that the sequence is regular except for the fact that catch in wind group 3 is slightly above that in wind group 2. The catch on nights of strong wind is only just above one-fifth of that on calm nights. The quite definite reduction in catch between nights of dead calm and nights with winds only 1-2 m.p.h. is unexpected, particularly as these very light winds are measured at about 70 feet above the ground. It was hardly expected that the difference would be noticed on the flight of insects within a few feet of the ground.

An examination of the meteorological records shows that there is a distinct association between wind force and minimum night temperature, and that, in general, windy nights are warmer than still nights. To study this effect the

mean temperature departures have been calculated for all the groups of nights as used above for catch classification and the results are shown in the second half of Table 30.

From the lower line of the table it will be seen that throughout the whole of the four years calm nights are distinctly cooler than windy nights. The most windy nights are about 1.5° F. above the normal and the calmest nights about 1.1° F. below normal, a total difference of about 2.6° F. This difference is most marked in the autumn, winter and spring months and is much less marked in the summer.



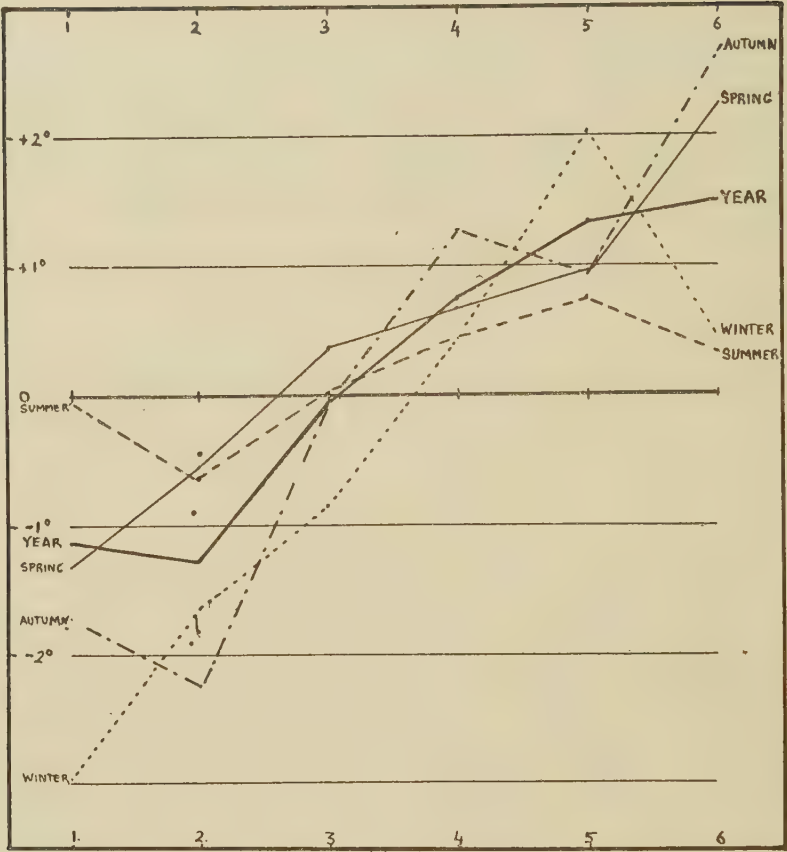
19

FIG. 19.—Departures from normal of the log. catch on nights of different wind intensity during the four years: (a) different seasons uncorrected for temperature; (b) all four years uncorrected for temperature; (c) different seasons corrected for temperature; (d) all four years corrected for temperature.

It will also be seen that on an average the nights with very slight winds (Group 2: 0-2 m.p.h.) were slightly colder than the dead calm nights and distinctly colder than the nights with stronger wind (2-5 m.p.h.).

The relation of wind to temperature is shown graphically in fig. 20.

Since it is known that minimum night temperature is affecting the catch, it follows that temperature and wind are normally working against one another, and that but for temperature the true wind effects would be greater than those shown. An approximate correction can be made by allowing a regression in



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FIG. 20.—Departures from normal of the minimum temperature on nights of different wind intensities during the four years.

TABLE 31.

Mean departure of catch, corrected for temperature, in each wind group in the different seasons.

Wind group					1	2	3	4	5	6
Spring					+0.33	+0.16	−0.03	−0.19	−0.29	−0.92
Summer					+0.24	−0.05	+0.02	−0.29	−0.66	−0.98
Autumn					+0.16	+0.14	+0.22	+0.02	−0.21	−0.68
Winter					+0.28	+0.31	+0.12	−0.01	−0.18	−0.38
Whole year {										
Log. dept.					+0.25	+0.13	+0.08	−0.09	−0.28	−0.60
Number					100	75	67	45	30	18
Calculated from {										
partial regression {					+0.28	+0.14	0	−0.14	−0.28	−0.42
Log. dept.					100	73	53	39	28	20
Number										

temperature of -0.75 per $^{\circ}\text{F}$., which has already been found to be near the truth. If this is done the final results are as shown in Table 31 and fig. 19, C and D.

An interesting point is that the bend in the uncorrected curve, due to Group 3 having a slightly higher mean catch than Group 2, is now eliminated and the new curve corrected for temperature is almost regular.

Fig. 21 (solid line) shows the actual numbers caught under different wind conditions (after correcting approximately for temperature) considering the catch at group 1 (dead calm) as 100.

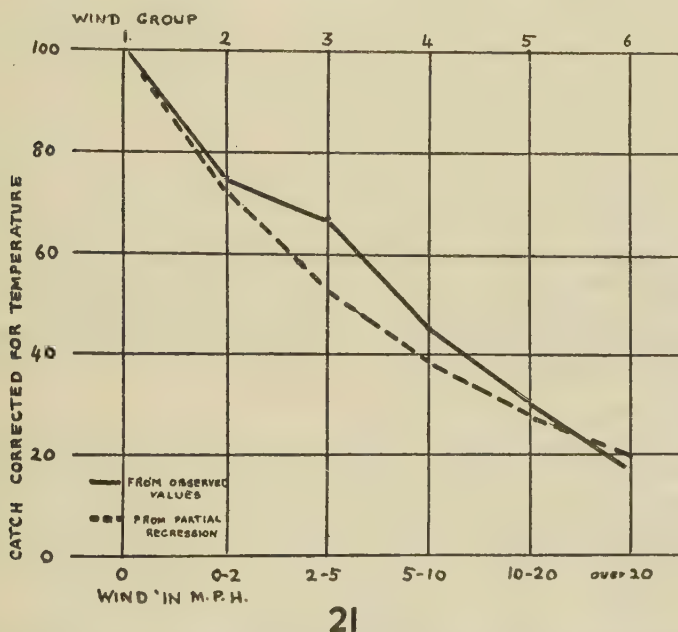


FIG. 21.—Catch of all insects on nights with winds of different intensities during the four years, expressed as percentages of the catch on dead-calm nights. Solid line giving results from mean catch on different nights with approximate correction for minimum temperature. Dotted line giving results from partial regressions on wind and minimum temperature.

As a check on the above, partial regressions of minimum temperature and wind group have been calculated from the above figures and give:—

Partial regression of log. catch on temperature . . . 0.074 per $^{\circ}\text{F}$.
 " " " " wind . . . -0.138 per wind group.

The catch for each wind-group calculated from the above regression is shown in the bottom rows of Table 31 and as a dotted line in fig. 21. The resemblance of the two series calculated by different methods from the available data is sufficiently close to show that the result is somewhere near the truth.

Calculations were also made of the regression of log. catch on wind by the method of difference between successive days. These are summarised in Table 32. They are of course uncorrected for associated temperature effects. The final results for the four years give a negative regression of -0.0946 ± 0.0113

TABLE 32.

Correlations and regressions of log. catch all insects and wind, by method of differences between successive days.

	Cor.	Reg.		Cor.	Reg.
Four March .	-0.36	-0.1517	Spring (11 months).	-0.29	-0.1226
April .	-0.29	-0.1158	Summer (11 months)	-0.28	-0.0946
May .	-0.22	-0.0920	Autumn . . .	-0.09	-0.0391
June .	-0.29	-0.0937	Winter .. .	-0.14	-0.0671
July .	-0.40	-0.1589			
Aug. .	-0.13	-0.0438	1933-34 . . .	-0.14	-0.0559
Sept. .	+0.02	+0.0046	1934-35 . . .	-0.27	-0.1045
Oct. .	-0.03	-0.0130	1935-36 . . .	-0.07	-0.0364 ± 0.0227
Nov. .	-0.20	-0.1042	1936-37 (10 months)	-0.24	-0.1200
Dec. .	-0.27	-0.1472			
Jan. .	-0.17	-0.0769	All four years (46 months) . . .	-0.18	-0.0946 ± 0.0113
Feb. .	+0.01	+0.0054			

per single group change, which is slightly lower than the result obtained from the departures from a 29-day mean.

(It will be seen later, p. 294, that when this regression is corrected for both maximum and minimum temperature it becomes - 0.144.)

For the month of July in all four years values were calculated for the mean catch of moths of the family NOCTUIDÆ for each of the wind groups. The results were as follows :—

Wind group	1	2	3	4	5	(6)
Log. catch departure						
NOCTUIDÆ . . .	+0.096	+0.013	+0.119	-0.155	-0.191	(-0.180)
Ditto for all insects . . .	+0.236	+0.058	+0.123	-0.379	-0.623	-0.840

The value for wind group 6 is from a single night and so is subject to considerable error.

It will be seen that the change in log. NOCTUIDÆ (from + 0.119 to - 0.191) is very much smaller than that for all insects (from + 0.236 to - 0.623, neglecting group 6), otherwise that the NOCTUIDÆ are much less affected by wind than the averages of all the other insects flying at the same time. The latter includes a very large number of small Diptera so that the result is in accordance with expectation.

Barometric pressure.

For the purpose of a preliminary analysis of the effect of barometric pressure on the catch, the nights in the six summer months (May to October inclusive) in each of the four years were divided into 9 categories according to whether the barometer was, on the one hand, rising, steady or falling; and on the other hand, high, medium or low. Medium barometer was taken to be between 29.9 and 30.2 inches. The barometer reading was that at midnight, taken from the chart of a recording barograph.

Table 33 shows the number of nights in each of these categories for each year and for the total of the four years, which included 703 nights on which data were available for both catch and barometer. The smallest total number of nights in any one category is 41 in the "low steady" class.

The departures of the log. catch for all insects from a running 29-day mean was entered for each night in its proper category, and the average departure for each category so obtained for each year and for all four years combined.

Table 34, A shows the results for the four years. It will be seen that the

TABLE 33.

Frequency of occurrence of different barometrical conditions. Top line in each successive year 1933-36; bottom line in all four years.

	Rising	Steady	Falling	
High .	14, 18, 17, 7 56	20, 25, 23, 25 93	18, 9, 11, 10 48	52, 42, 51, 42 187
Medium .	30, 25, 22, 23 100	28, 29, 28, 28 113	33, 31, 33, 23 120	91, 85, 83, 74 333
Low .	16, 27, 19, 19 81	6, 9, 14, 12 41	14, 19, 17, 11 61	36, 55, 50, 42 183
	60, 60, 58, 49 227	54, 63, 65, 65 247	65, 59, 61, 44 229	179, 182, 184, 158 703

"high rising" barometer gives the highest catch with a log. departure of + 0.21 above the normal, while "low rising" gives the lowest catch with - 0.37 below the normal.

Table 34, B shows the same figures converted into percentages of a normal catch. Above-normal catches are obtained with high barometer if rising, or steady, and with medium barometer if steady or falling. Below-normal catches are obtained with low barometer; with medium barometer if rising; and with high barometer if falling. This latter result is somewhat unexpected but it occurs in each of the four years of which the table shows the combined total.

The lowest average catch is 43% of the normal (with low barometer rising), the highest average catch is 162% of the normal (with high barometer rising). If the direction of movement is neglected the average catches under high, medium and low barometer are 135; 120; and 51 respectively. If the height of the barometer is neglected the average catches with rising, steady and falling barometer are 74; 129; and 115.

TABLE 34.

Departure of log. catch all insects from normal under various barometrical conditions, in all four years.

	A Catch (log. dept.)				C Min. temperature				E Wind			
	Ris.	Stdy.	Fall.		Ris.	Stdy.	Fall.		Ris.	Stdy.	Fall.	
High .	+0.21	+0.20	-0.07	+0.13	-1.6	+0.5	+0.5	-0.01	2.1	2.3	2.3	2.2
Medium .	-0.10	+0.17	+0.14	+0.08	-2.1	+1.3	+1.6	+0.4	2.3	2.2	2.7	2.4
Low .	-0.37	-0.28	-0.19	-0.29	-2.2	-0.6	+1.4	-0.6	3.3	3.0	3.7	3.3
	-0.13	+0.11	+0.06		-2.1	+0.7	+1.3		2.6	2.4	2.9	2.6
	B Catch (%)				D Catch corr. for temp.				F Catch (%) corr. for temp. and wind			
	Ris.	Stdy.	Fall.		Ris.	Stdy.	Fall.		Ris.	Stdy.	Fall.	
High .	162	159	85	135	213	144	77	134	177	125	67	114
Medium .	79	148	138	120	114	119	104	111	100	101	104	101
Low .	43	52	65	51	62	57	49	57	78	65	70	72
	74	129	115		106	114	90		106	101	100	

In order to see to what extent these differences might be explained by other factors known to be associated with special barometrical conditions, the departures from the normal for minimum temperatures and the average wind intensity (in 6 groups as explained on p. 278) was worked out for each of the nine categories and are shown in Table 34, C and 34, E. With this information and a knowledge of the approximate effect of unit change of temperature and wind (see pp. 262 and 283), it is possible to make a correction for the effect of these factors on the catch, either separately or together.

Table 34, D shows the log. departures for the catch corrected for minimum temperature and converted into percentages; and Table 34, F shows the results corrected for both temperature and wind.

It will be noted that after these corrections have been made low barometer is still associated with low catches; medium barometer gives results almost normal; while high barometer gives catches above normal if the barometer is rising or steady, but well below normal if the barometer is falling. The difference between rising and falling has been much reduced except in cases of high barometer.

Neglecting the direction of movement, the catches with high, medium and low barometer are now 114, 101 and 72 (135; 120 and 51 before correction); and neglecting the height of the barometer the catches with rising, steady and falling barometer are 106, 101 and 100 (74; 129; and 115 before correction).

The low catch with high falling barometer still persists after correction for wind and minimum temperature and is difficult to explain.

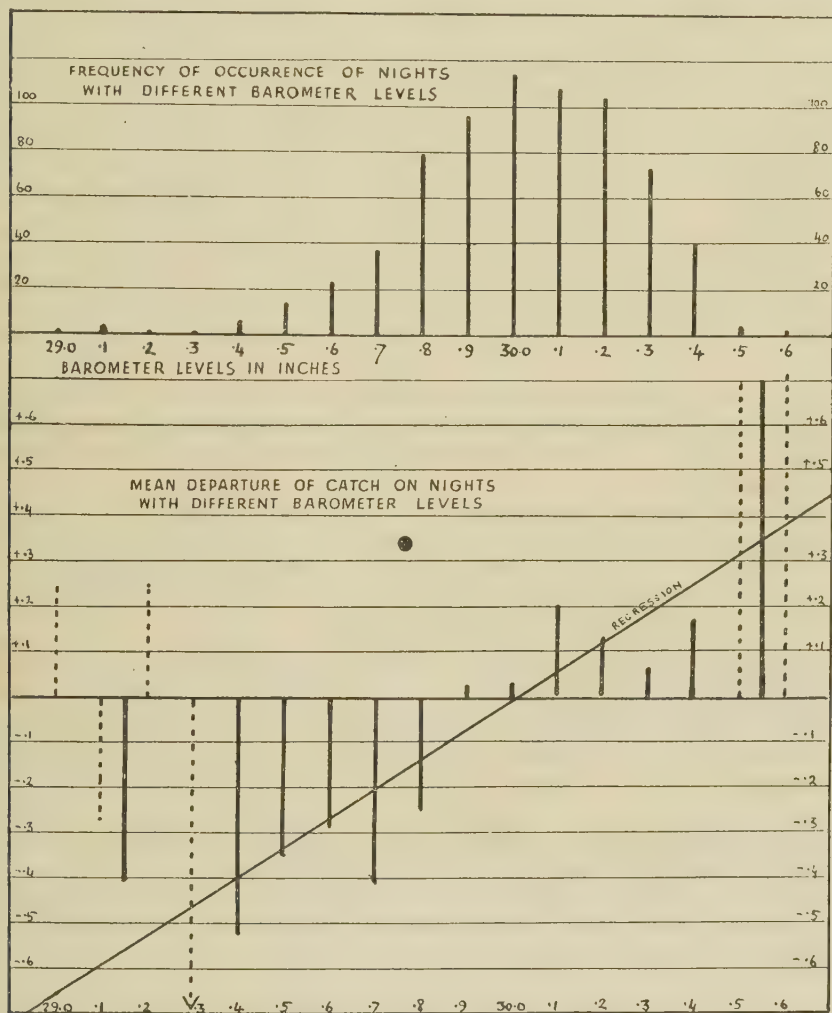
A more complete analysis of the effect of height of barometer, independent of the direction of movement, is shown in Table 35 and fig. 22. On these are shown first the frequency of occurrences of nights with different barometer levels at midnight. It will be seen that the lowest barometer level observed during the four summers was 29.0 inches (recorded once only) and the highest 30.6 inches (recorded twice). The most frequent level is 30 inches, and the curve of distribution is not symmetrical.

TABLE 35.

Frequency of occurrence of different barometrical levels in the summer months of all four years and the mean log. catch departure from normal on these nights.

Barometer level at midnight	Number of occurrences	Mean catch departure
29.0 inches	1	(+0.25)
0.1	4	-0.27
0.2	1	(+0.25)
0.3	1	(-1.73)
0.4	6	-0.52
0.5	14	-0.35
0.6	23	-0.29
0.7	37	-0.41
0.8	79	-0.25
0.9	95	+0.03
30.0	114	+0.03
0.1	108	+0.20
0.2	104	+0.13
0.3	73	+0.06
0.4	40	+0.17
0.5	4	+0.70
0.6	2	(+0.72)

The lower histogram in fig. 22 shows the mean departures of the log. catch from the normal for all the nights with each of these barometer levels. The values obtained from fewer than five readings are shown dotted, with a solid line between those showing the average for all the high and all the low values of this character.



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FIG. 22.—Effect of barometric pressure on catch. Above: frequency of occurrence of nights with different barometer levels in six summer months for four years. Below: mean catch on nights of different barometer levels and regression of catch on pressure.

The regression of the rate of change of catch per unit change of temperature has been calculated from the whole of the available data for the four years and is 0.668 change in log. catch per inch change of barometer. Otherwise a rise of barometer of 0.45 inch is equivalent to adding 0.30 to the log., which is equivalent to doubling the catch.

The regression line is shown across the histogram in fig. 22.

Thunder and lightning.

Thunder and lightning were recorded by the meteorological observers on 40 days during the summer months of the four years. Nearly all cases occurred in the late afternoon or evening. The days were distributed as in Table 36.

TABLE 36.

Frequency of occurrence of thunderstorms in the six summer months of the four years.

	1933	1934	1935	1936	Total
May	1	2	2	1	6
June	4	2	2	4	12
July	2	3	2	4	11
August	0	1	0	1	2
September	1	2	2	1	6
October	0	0	2	1	3
Total	8	10	10	12	40

The mean log. catch of all insects on the nights following these days (averaged from departures from a 29-day mean) was -0.057 , equivalent to a catch of 12% below normal. As the standard error of the mean is ± 0.097 the difference is not significant.

The mean log. catch of all insects on the night previous to these days, *i.e.* the catch during the conditions just preceding thundery weather is $+0.053$ or about 13% above normal. But again the difference is not significant.

If, however, one deals with moths of the family NOCTUIDAE instead of all insects one gets a significant difference as follows.

On the nights following days with thunder the log. catch of NOCTUIDAE (again from departures from a 29-day mean) is $+0.076$ (or 19%) above normal, with a standard error of ± 0.023 .

On the nights preceding thundery weather the log. catch of NOCTUIDAE is $+0.094$ (equivalent to a catch of 24% above normal) with a standard error of ± 0.021 .

That these results are not simply due to temperature is shown by the fact that the average minimum temperature on both days preceding and days following the thundery weather was 0.5° F. below normal.

The figures therefore lend a certain amount of support to the idea widespread among collectors of Lepidoptera that moths may be captured more abundantly during conditions of thundery weather.

ANALYSIS OF SEVERAL FACTORS SIMULTANEOUSLY.

Interrelation of climatic factors.

Owing to the fact that the different climatic factors are themselves correlated, as previously outlined on p. 242, each factor does not appear to produce the same effect when it is considered singly, neglecting the others, as when it is considered together with other factors and the effect of each is assessed independently. Thus I have found that a rise of one degree in minimum temperature (neglecting maximum) is associated with an increase in log. catch of 0.060, while an increase of one degree in maximum temperature (neglecting minimum) is associated with an increase in log. catch of 0.042. But it is known

that, in general, warm days are followed by warm nights—or, in other words, that there is a positive correlation between the two—so that some of the effect found on warm nights must be due to the warmth of the previous day, and some of the effect credited to the maximum temperature must be due to the following minimum. Thus when an analysis is made that assesses independently the effect of two positively correlated factors (such as maximum and minimum) the effect of each is slightly less than when they are considered independently. If, on the other hand, they are negatively correlated (or if the correlation of one with the trap is positive and the other negative) then the new values will be larger than before. The more closely the climatic factors are correlated the more difficult it is to assess to each their proper value. The mathematical process necessary is that of “partial regressions” and will be found described in any statistical textbook.

For an understanding of the results, however, it is necessary to realise the extent to which the climatic factors are themselves correlated.

Values for the correlation of the four factors, maximum and minimum temperature, wind and 9 p.m. relative humidity, are shown in Table 37, based on the results of all four years.

TABLE 37.

Correlation of temperature, wind force and relative humidity, based on difference of successive days over four years.

	Max. T.	Wind	R.H. 9 p.m.
Minimum temperature	+0.32	+0.32	+0.04
Maximum temperature	—	+0.18	—0.18
Wind	—	—	—0.08

It will be seen that the correlations are positive between maximum and minimum temperature and wind; negative between 9 p.m. R.H. and maximum temperature (in other words, the hotter the previous day the dryer the evening); negative but of doubtful significance between wind and 9 p.m. relative humidity; and doubtfully positive between minimum temperature and 9 p.m. relative humidity.

The correlation between the minimum temperature on one night and that of the previous night on 12 summer months (351 days) is 0.36, while with the night before that (2 nights previous) the correlation is only 0.13.

Other correlations have already been mentioned but have not been calculated as a mathematical expression. Thus cloudy nights have higher minimum temperature: the minimum temperature is slightly higher with a falling barometer than with a rising one (probably owing to the effect of cloud); and the wind is greater with a low barometer than with a high barometer.

It is these numerous interrelations that make the analysis of the partial regressions which follows so difficult and which gives the results relatively high errors in spite of the large number of observations on which they are based.

Temperature, moon and cloud.

An examination has been made to see if the regression of log. total insects on minimum temperature is different under different conditions of cloud and moonlight. Unlike all the others which follow, this was not done by partial regressions but by dividing the nights up into the nine moon-cloud categories

as already explained (p. 274) and then calculating the regressions on temperature for each group, and for combinations of groups.

The results for the three years 1933-35 are shown in Table 38. In each square the upper figure is the total number of days in that category; the number on the left is the correlation; and the number on the right the regression. It will be seen that there are no large differences between the groups, except that all cloudy nights give a regression of 0.023 while all intermediate and all clear nights give a regression of 0.051 and 0.053. When, however, the errors are calculated, it is found that the difference between cloudy and intermediate is 0.028 and the error of the differences 0.0175. The difference is therefore 1.6 times the standard error and not significant, as once in ten times this difference could be obtained by chance.

There is therefore, from these data, no proof of a difference of regression under different conditions of cloud and moon.

TABLE 38.

Correlations and regressions of log. catch on minimum temperature in the three years 1933-35, in different cloud and moon conditions.

	Clear		Intermediate		Cloudy	
	Cor.	Reg.	Cor.	Reg.	Cor.	Reg.
Full moon	45 0.47	0.057	43 0.34	0.059	30 0.14	0.023 0.39
First and last quarter	82 0.42	0.049	107 0.36	0.050	56 0.13	0.020 0.36
New moon	41 0.61	0.060	46 0.26	0.035	37 0.21	0.032 0.42
	168 0.47 ±0.010	0.053	196 0.34 ±0.010	0.051	123 0.15 ±0.014	0.023

Minimum temperature on previous nights.

Calculations have been made to show to what extent the catch is affected by the minimum temperatures of the nights previous to the one on which the catch is made.

Table 39 shows the partial regressions of log. total catch of all insects on the minimum temperature of the current night, the previous night and the night before that. Also, for comparison, the regression on the current night only.

It will be seen that on the total twelve summer months the effect per degree for the current night is 0.0662 and for the previous night 0.0150, while the regression on the second night previous is very small indeed and not significant.

Thus if the two nights only are considered, about four-fifths of the effect is due to the temperature on the current night and about one-fifth to that on the previous night.

An analysis of variance shows that the mean trap variance is 0.387 per day, of which 0.282 is residual error when allowance has been made for the three regressions. Approximately 27% of the total variance is accounted for by these regressions. When, however, the residual variance is calculated from the

simple regression on minimum temperature for the current night only the residual variance is almost exactly the same—0.284.

This shows that little or no gain in accuracy in prediction is obtained by using the extra information from the previous night.

TABLE 39.

Regressions and partial regressions, all insects (log. departure from monthly means) and minimum temperature, in three summer months of four years.

	Regression on current night only	Partial regressions on		
		Current night	Previous night	2nd night previous
May 1933	0.1107	0.1004	0.0322	0.03006
1934	0.107	0.0952	0.0295	—0.01030
1935	0.106	0.1113	—0.0111	0.00352
1936	0.0965	0.0898	0.0067	0.03270
All 4 Mays	0.1052	0.0981	0.0089	+0.0097
All 4 Julys	0.0598	0.0579	0.0118	—0.01649
All 4 Septembers	0.0561	0.0504	0.0170	—0.00047
12 months as above	0.0716	0.0662	0.0150	+0.00041

Temperature at 9 p.m. and different methods of expressing humidity.

For the months of June and July 1933 calculations were made of the partial regressions for the total catch on 9 p.m. temperature and the 9 p.m. humidity. The latter was expressed in three different ways: (1) Relative Humidity as percentage, (2) Saturation Deficiency (in inches), and (3) Absolute Humidity as Vapour Pressure in inches (see p. 241).

It will be seen from Table 40 that the regression on temperature is lowest in both months when vapour pressure is the second factor, and highest when saturation deficiency is the second factor. Further, in June the mean variance is 0.2782 and the residual variance is lowest with saturation deficiency and highest with vapour pressure. In July the residual variance is lowest with relative humidity and highest with vapour pressure.

In June 1933 a further calculation was made, using the insects in the first period of the night only as the dependent variable. These were the insects caught round about 9 p.m., when the temperature and humidity observations were taken. This again shows the highest temperature effect with saturation deficiency and the lowest with vapour pressure; on the other hand, the analysis of variance shows the lowest residual variance when using vapour pressure.

The figures indicate that for the purpose of this type of analysis, there is very little difference in accuracy of result to be obtained by using any one method in preference to another.

This being the case, calculations were completed for partial regressions of total catch on 9 p.m. temperature and 9 p.m. relative humidity for the fifteen months, May 1933–July 1934. (After the latter month the 9 p.m. observations were unfortunately discontinued.) The results are shown in Table 41. For the whole year, the partial regression on minimum temperatures was 0.0834 per degree and on relative humidity 0.0164 per 1% change. Thus 1° F. has the same effect as 5.6% change in relative humidity. Also a rise of either 3.4° F. or 18% in relative humidity will double the catch.

TABLE 40.

Comparison of partial regression of catch on temperature and on different methods of expressing the humidity of the atmosphere, all from departures from monthly means.

1933		June		July	
		Regression on		Regression on	
		Temp.	Moisture	Temp.	Moisture
Total catch :					
	Mean variance . . .		0.2782		0.4327
9 p.m.	Temp. and rel. humidity . . .	0.124	0.0327	0.155	0.0283
	Residual variance . .		0.0860		0.1739
9 p.m.	Temp. and sat. deficiency . . .	0.159	—0.300	0.177	—0.186
	Residual variance . .		0.0766		0.1750
9 p.m.	Temp. and vapour pressure . . .	0.041	0.0650	0.086	0.0394
	Residual variance . .		0.1068		0.1843
Catch in 1st period only :					
	Mean variance . . .		0.3502		
9 p.m.	Temp. and rel. humidity . . .	0.1005	0.0215		
	Residual variance . .		0.2233		
9 p.m.	Temp. and sat. deficiency . . .	0.1234	—0.1923		
	Residual variance . .		0.2240		
9 p.m.	Temp. and vapour pressure . . .	0.0411	0.0560		
	Residual variance . .		0.2132		

The mean variance of the catch for this year was 0.4139 and the residual variance after subtracting the effects of 9 p.m. temperature and 9 p.m. relative humidity was 0.2616, showing that about 37% is accounted for. This is higher than the figure 24% obtained by using maximum and minimum temperature (see p. 293), but the latter was on four years analysis while this is only on one year.

TABLE 41.

Partial regressions of log. total catch on 9 p.m. temperatures and relative humidity (from departures from monthly means).

			Temp.	Rel. H.				Temp.	Rel. H.
1933	May	.	0.1307	0.0048	1934	May	.	0.0762	0.0035
	June	.	0.1235	0.0327		June	.	0.0554	0.0025
	July	.	0.1545	0.0283		July	.	0.0810	0.0037
	Aug.	.	0.0700	—0.0001	Six summer months, May to Oct. 1933				
	Sept.	.	0.0594	0.0165					
	Oct.	.	0.0505	0.0741	Six winter months, Nov. 1933–April 1934				
	Nov.	.	0.0830	0.0422					
1934	Dec.	.	0.1450	0.0301	Year, May 1933 to April 1934				
	Jan.	.	0.0564	0.0246					
	Feb.	.	0.0531	0.0079	0.0834 0.0164				
	March	.	0.0907	0.0132					
April	.	0.0869	0.0097	Mean variance for whole year = 0.4139 Residual variance = 0.2616					

Maximum and minimum temperatures.

The individual effect of maximum and minimum temperature, acting simultaneously, on the total catch of all insects is shown by the partial regressions in Table 42.

It will be seen that the average effect over the four years is 0.0539 per degree minimum temperature and 0.0215 per degree maximum. These are both smaller than the single regressions but this is to be expected as the maximum and minimum temperatures are themselves correlated and their effects are both positive.

TABLE 42.

Partial regressions of log. catch on maximum and minimum temperatures (from differences between successive days) with simple regressions for comparison.

All four years	Partial regressions		Simple regressions for comparison	
	Minimum	Maximum	Minimum	Maximum
March	0.0704	-0.0095	0.069	0.005
April	0.0302 $\pm$ 0.0129	0.0305 $\pm$ 0.0131	0.042	0.043
May (3)	0.0664	0.0179	0.074	0.038
June (3)	0.0700 $\pm$ 0.0136	0.0278 $\pm$ 0.0108	0.080	0.044
July	0.0460	0.0342	0.050	0.039
August	0.0539 $\pm$ 0.0107	0.0275 $\pm$ 0.0105	0.063	0.045
September	0.0405	0.0272	0.045	0.043
October	0.0627 $\pm$ 0.0115	0.0109 $\pm$ 0.0200	0.066	0.063
November	0.0556	0.0022	0.056	0.022
December	0.0400 $\pm$ 0.0232	0.0673 $\pm$ 0.0245	0.060	0.091
January	0.0511	0.0267	0.063	0.055
February	0.0819 $\pm$ 0.0170	0.0089 $\pm$ 0.0167	0.079	0.017
All 4 years . .	0.0539 $\pm$ 0.0038	0.0215 $\pm$ 0.0044	0.060	0.042

Analysis of variance shows that the total mean variance of the trap is 0.5885 per day, of which 0.1390 (24%) is accounted for by the two partial regressions. With the single regression 0.0964 (16%) is accounted for by minimum temperature only, and 0.0350 (6%) by maximum temperature only.

Calculations have also been made of the partial regressions on maximum and minimum temperature for the 4 summer months (June to September) for the catches of Lepidoptera only. They are shown in Table 43. It will be seen that the values per degree are smaller with the Lepidoptera only than

TABLE 43.

Partial regressions of Lepidoptera only on maximum and minimum temperature, in the four summer months of all four years, with figures for all insects for comparison.

Lepidoptera only	Partial regressions	
	Minimum	Maximum
June (3)	0.063 $\pm$ 0.011	0.031 $\pm$ 0.009
July (4)	0.041	0.030
August (4)	0.042	0.019
September (4)	0.026	0.014
Four summers (15 months)	0.0373 $\pm$ 0.0039	0.0251 $\pm$ 0.0041
Four summers. All insects for comparison	0.0484 $\pm$ 0.0052	0.0304 $\pm$ 0.0056

with the total catch all insects, but that the difference in the value for minimum temperature is barely significant and the difference for the maximum temperature is quite definitely not significant.

Simultaneous effect of maximum and minimum temperature and wind.

Table 44 shows the partial regressions on maximum and minimum temperature and wind, calculated by the method of differences between successive days over the four years.

It will be seen that there is little difference between the regressions on minimum temperature in the four seasons; with the maximum temperature spring and autumn are low and summer and winter higher, but the differences are doubtfully significant; with the wind, spring gives a higher value and autumn low, but again the differences are only just on the verge of significance and might be due to accident. More results must be obtained before these points can be settled.

For the whole period of the four years the regression on minimum temperature is 0.0696 ± 0.0038 ; on maximum is 0.0225 ± 0.0042 and on wind -0.1439 ± 0.0103 . Thus the catch is doubled by an increase of minimum temperature of about 4.4° F. ; by an increase in maximum temperature of about 13.4° F. ; and by a change of wind of approximately two groups. Each of these is of course considered as acting quite independently of the others and free from the normal correlation that exists between them.

Analysis of variance shows that the mean trap variance over the four years is 0.5775, and after allowing for the three regressions the residual variance is 0.4170 or 72%. Thus 28% of the variance is accounted for by these three factors over the four years.

TABLE 44.

Partial regressions of log. catch on maximum and minimum temperature and wind for the four years 1933-37, from differences between successive days.

	Minimum temp.	Maximum temp.	Wind
Spring (March-May) .	0.0739	0.0128	-0.1883
Summer (June-Aug.) .	0.0654	0.0307	-0.1423
Autumn (Sept.-Nov.) .	0.0680	0.0185	-0.1283
Winter (Dec.-Feb.) .	0.0709 ± 0.0093	0.0262 ± 0.0105	-0.1344 ± 0.0233
All 4 years [†] . .	0.0696 ± 0.0038	0.0225 ± 0.0042	-0.1439 ± 0.0103

Simultaneous effect of four factors : maximum and minimum temperature, wind and 9 p.m. relative humidity.

For the year 1933-34 data were available to calculate the simultaneous effect of four factors which are shown in Table 45. That on minimum temperature is 0.0652 ± 0.0075 ; on maximum 0.0164 ± 0.0077 ; on wind 0.1209 ± 0.0203 , and on relative humidity 0.0063 ± 0.0033 . The regression on humidity is just significantly positive. It is small because of the small unit taken, which is 1% change in relative humidity.

The catch is therefore doubled by 4.6° F. rise in minimum temperature; by 18° F. rise in maximum temperature; by 2.5 fall in wind group and by 47% change in relative humidity.

Analysis of variance shows that out of a mean variance of 0.4921, the

residual is 0.3742 or 76%. Thus about 24% of the variance is accounted for in this year by the four factors.

If relative humidity is neglected and only the other three factors are used for this year the values of the regressions are shown in the last column of Table 44. In this case the residual variance is 0.3781, which is practically indistinguishable from the result with four factors. Thus little or no increase in accuracy of estimation is obtained by adding relative humidity to the list of factors.

TABLE 45.

Partial regressions of log. catch on four weather factors, for year March 1933 to February 1934, from differences between successive days.

	Regression	Three factors only
Minimum temperature . . .	+0.0652 $\pm$ 0.0075	0.0670
Maximum temperature . . .	+0.0164 $\pm$ 0.0077	0.0133
Wind . . .	-0.1209 $\pm$ 0.0203	0.1250
Rel. humidity at 9 p.m. . .	+0.0063 $\pm$ 0.0033	—

Analysis of variance.

I have shown that the effect of different weather conditions on the catch of insects in the trap can be analysed; first for single factors, then for two simultaneously, and finally for three and four factors acting together.

Any factors which can be expressed numerically can be added to the analysis but as each new variable is included for the same trap data, the labour of calculation and the error of assessing the values both become greater. This is particularly so when, as is usually the case, the climatic factors are themselves highly correlated.

I start with the variableness or "variance" of the trap catch, as much as possible of which it is desired to explain.

Using the catch expressed as log. ($n + 1$) and the method of differences between successive days the total variance (sum of square of differences) in the four years is 775.5919. This is on 1343 days and the mean variance is therefore 0.5775. Otherwise the mean change of the catch from one day to the next throughout the four years was 0.76 (the square root of the mean variance).

This variance is caused by:—

- (1) changes in activity due to weather;
- (2) error of estimation due to using a single trap;
- (3) lunar effect;
- (4) population changes not eliminated by using differences between successive days;
- (5) other causes which must be grouped together as "error."

(1) Using the triple regressions on minimum temperature, maximum temperature and wind (p. 294) I can account for a variability during the four years of 217.7206.

(2) It is shown on p. 234 that the error per night by using a single trap was, on the method of differences, 0.2619 with a variance of 0.0686. This for the 1343 nights accounts for a variance of 92.1298. It is extremely likely that this is an under-estimation as only two months data (September and October 1933) were available from which it could be calculated. During this

period catches were relatively high. I should expect greater differences between the catches of the two traps in the winter, when catches are low.

(3) The lunar effect is very regular and has been shown (p. 272) to vary for all insects between the extremes of -0.18 and $+22$, or a change of 0.40 in a half lunar period of about 14 days. The change, however, is probably more extreme in autumn and spring than in summer and winter. It has already been shown to average approximately 0.0033 per day. This would on the 1343 days only account for 4.4319 of the total variance.

(4) Population changes have been eliminated as far as possible by using differences between successive days, but even this method will not allow for sudden emergence of large numbers of adults for the chrysalis, or for sudden destruction of large numbers by frost, rain or other causes. There is therefore a residual error from this cause which it does not seem possible at present to assess.

The balance sheet, or analysis of variance as it is termed in statistics, is as follows:—

	Degrees of freedom	Total variance	Mean variance
All sources	1341	775.5919	0.5775
Temperature and wind	3	217.7206	
Trap error	1	92.1298	
Moon	1	4.4319	
Residual	1336	461.3096	$0.3453 = 60\%$ of original

Thus 60% of the variance still remains unexplained as "error."

Table 46 and fig. 23 show how the mean variance changes from month to month for both trap, temperature and wind. It will be seen from this that the variance of the trap makes a very sudden rise in October and November and remains

TABLE 46.

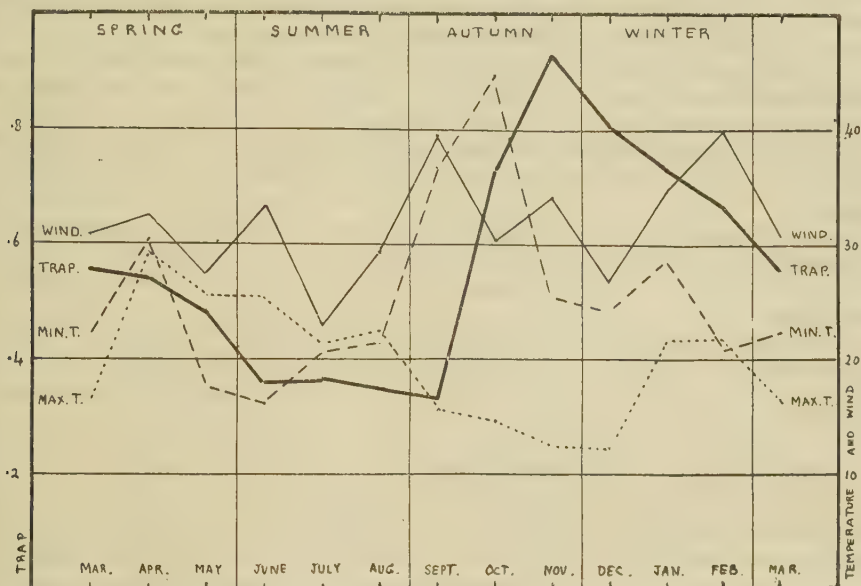
Mean variance per day of trap, maximum and minimum temperature and wind, from differences between successive days.

	Trap	Min. T.	Max. T.	Wind		Trap	Min. T.	Max. T.	Wind
March .	0.5570	22.05	16.55	3.09	Spring .	0.5283	23.92	23.84	3.05
April .	0.5358	30.50	29.46	3.26	Summer .	0.3591	19.61	22.82	2.81
May .	0.4834	17.81	25.66	2.73	Autumn .	0.6655	35.83	14.11	3.47
June .	0.3599	16.08	25.32	3.33	Winter .	0.7372	24.76	18.37	3.35
July .	0.3689	20.54	21.43	2.30					
Aug. .	0.3485	21.36	22.31	2.92	1933-34 .	0.4921	24.27	20.33	3.07
Sept. .	0.3339	36.94	15.61	3.97	1934-35 .	0.4926	25.56	21.56	3.29
Oct. .	0.7315	44.80	14.71	3.02	1935-36 .	0.6190	28.50	17.54	3.37
Nov. .	0.9345	25.43	12.27	3.43	1936-37 .	0.7353	25.59	18.75	2.94
Dec. .	0.8038	24.04	12.01	2.68					
Jan. .	0.7317	28.69	21.70	3.48	All 4 years .	0.5775	26.21	19.58	3.18
Feb. .	0.6660	20.97	21.88	4.00					

at a high level during the winter. The mean variance for the four Novembers is 0.9345 , which is nearly three times the value for September, when it is lowest. It is during the months of October, November and December that very great numbers of TRICHOCERIDAE (winter-gnats) come into the trap. In fact the mean catch of the trap for November (average of four years) is actually above that of October, in spite of the fall of temperature. Undoubtedly this introduces new factors into the problem the effect of which is at present difficult to estimate.

One of them is undoubtedly a much higher humidity effect, as the *Trichocera* are in very great abundance on damp nights. The effect of this is shown in Table 22 (p. 268) in the much higher regression of insects on humidity in the autumn than at any other period.

If, therefore, one considers that some abnormal factor makes it incorrect to apply the same variance and the same regression to all times of the year,



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FIG. 23.—Annual sequence of variability in the trap catch and in some weather factors; all calculated from difference between successive days.

one may compare with the whole year's analysis of variance just given that for the three summer months from June to August only as follows :—

	Degrees of freedom	Total variance	Mean variance
All sources	326	117.0773	0.3591
Temperature and wind	3	46.9918	
Trap	1	22.3636	
Moon	1	1.0758	
Residual	321	46.6461	0.1453 = 40%

In this case the residual error is only 40%, so that 60% is explained on the known sources of variability.

ESTIMATION AND FORECASTING OF THE POPULATION.

Estimation.

In the previous portion of this paper I have shown that the catch is dependent on both activity and population, and an attempt was made to estimate the effect of activity by eliminating as far as possible the effects of population. The object of the present section is to see if it is possible to perform the reverse operation which is to eliminate the activity effects and so estimate the population changes.

I have shown that the effect of maximum and minimum temperatures, of wind and of relative humidity can be expressed by certain regression values giving the effect on the dependent variable (the catch) of unit change in the independent variable. As these values have been calculated from differences between successive days, they are believed to consist very largely of the activity effect, and to exclude as far as possible longer trends of population change.

The mean log. catch for the month of March in all four years was 0.88, while the mean catches in March in each of the four successive years were 0.97; 0.56; 1.13 and 0.87 respectively. Thus the mean catches departed from their own average by + 0.09; - 0.32; + 0.25 and - 0.01 respectively, as shown in the first column of Table 47.

Part of these differences must be due to the different activity in March of each year, owing to weather conditions; and part to the fact that the population was not always the same. If one considers that other errors are as likely to be positive as negative, the total departure for each month must be made up of the change in activity due to the current weather conditions plus the change in population due, as will be discussed later, largely to previous weather conditions.

But since both the effect of unit change in each of the principal weather conditions on activity, and the extent to which the weather conditions varied from the mean in each month are known, it should be possible to correct for these departures in activity and be left with a value for the catch which would have been obtained under standard conditions. Changes in this should be a measure of population change.

If reference be made to Table 2 (p. 231) it will be seen that in March 1933 the minimum temperature was 0.1° F. below the normal for the four years and the maximum temperature was 3.3° F. above normal. The wind value was 0.27 below normal. From Table 44 will be found the partial regression values for each of these factors. From these two sets of figures it will be seen that the expected departure from normal of the catch in March 1933, due to activity factors is:—

$$\begin{array}{rcl}
 0.1 \times 0.070 & = & + 0.007 \text{ for the minimum temperature} \\
 3.3 \times 0.0225 & = & + 0.076 \text{ for the maximum temperature} \\
 - 0.27 \times - 0.144 & = & + 0.039 \text{ for the wind force} \\
 \hline
 \text{Total} & = & + 0.122
 \end{array}$$

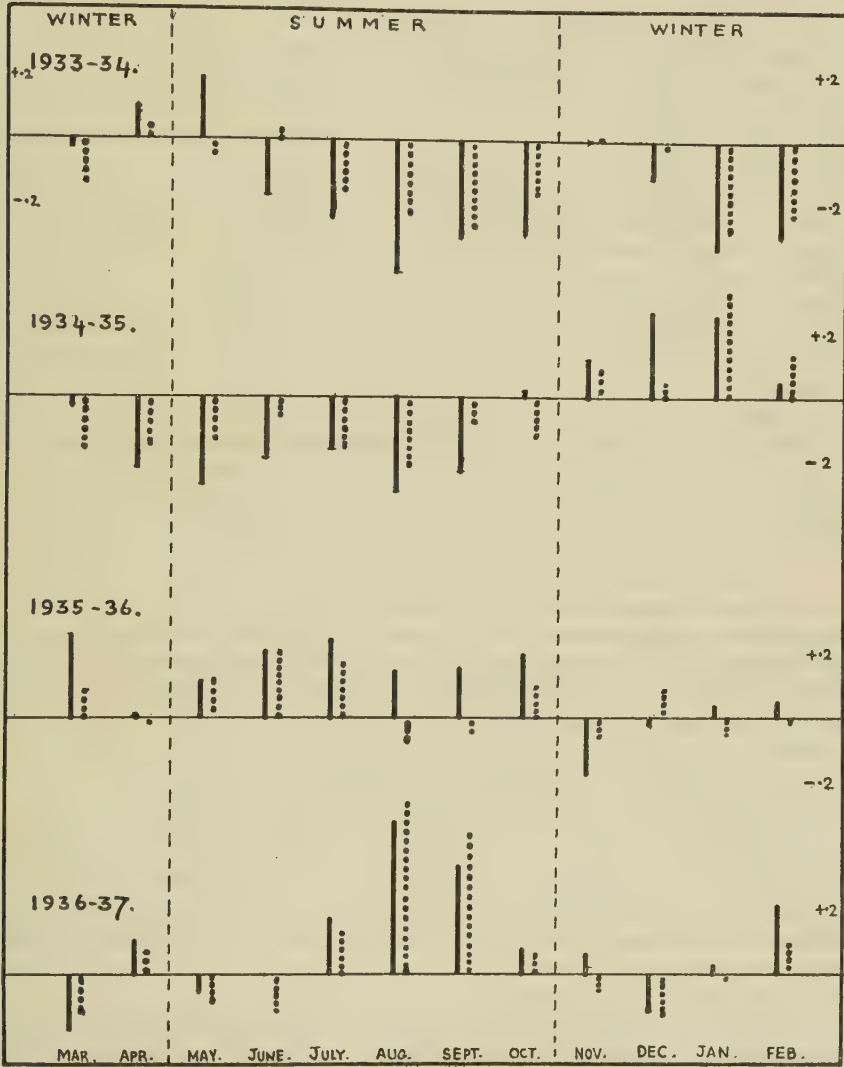
Otherwise that owing to the weather conditions during March the catch would be expected to be 0.12 above normal if the population were normal. Actually the catch was 0.09 above normal or - 0.03 below the expected value. If this reasoning be correct, and no major factor is left out, this - 0.03 should be a measure of the population change from normality for March 1933. Similar calculations give - 0.03, + 0.26 and - 0.17 for March in 1934, 1935 and 1936.

In Table 47 is shown first of all the observed departure from the mean in each of the 48 months; next the expected departure owing to the effect of maximum and minimum temperature and wind, and finally the difference between these two which is presumed to be the measure of the population changes.

The series of values so obtained are shown graphically by the vertical solid lines in fig. 24.

It will be seen that they suggest that for the first month (March 1933, just discussed in detail) the population was almost normal; for the next two months

it was above the normal for that time of the year; and then followed a long period of seventeen months in which the population continued below normal. This spell lasted from June 1933 to September 1934, and, as will be seen by



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FIG. 24.—Mean log. population departure from the normal in the 48 months. Solid line calculated by correcting the mean log. catch for each month for the departure of the weather conditions from the normal. Dotted line forecasted from the weather conditions of previous months by regression formulae.

comparison with Table 2 (p. 231), it corresponded with a long drought which started in June 1933 with the rainfall 1.90 inches below the normal and continued until July 1934. August 1934 was the first month with the rainfall above normal (+ 0.74) and by October the population had returned to normal.

TABLE 47.

Data for the correction of the mean log. catch for any one month for the departure of the weather conditions of that month from the normal.

	Observed departure of mean log. catch from mean of same month in all four years (a)				Expected activity effect of maximum and minimum temperature and wind (b)				Difference between observed and calculated (a - b)			
	1933	1934	1935	1936	1933	1934	1935	1936	1933	1934	1935	1936
Winter :												
March . . .	+0.09	-0.32	+0.25	-0.01	+0.12	-0.29	-0.01	+0.16	-0.03	-0.03	+0.26	-0.17
April . . .	+0.23	-0.09	±0	-0.13	+0.12	+0.13	-0.01	-0.24	+0.11	-0.22	+0.01	+0.11
Summer :												
May . . .	+0.46	-0.31	-0.18	+0.02	+0.26	-0.04	-0.30	+0.08	+0.20	-0.27	+0.12	-0.06
June . . .	-0.15	-0.15	+0.20	+0.09	+0.02	+0.04	-0.01	+0.09	-0.17	-0.19	+0.21	±0
July . . .	-0.12	-0.08	+0.29	-0.08	+0.12	+0.08	+0.04	-0.26	-0.24	-0.16	+0.25	+0.18
August . .	-0.28	-0.50	+0.25	+0.57	+0.15	-0.21	+0.10	-0.03	-0.41	-0.29	+0.15	+0.48
September .	-0.20	-0.22	-0.02	+0.42	+0.10	+0.01	-0.18	+0.08	-0.30	-0.23	+0.16	+0.34
October . .	-0.20	+0.13	+0.10	-0.02	+0.09	+0.11	-0.10	-0.10	-0.29	+0.02	+0.20	+0.08
Winter :												
November .	+0.01	+0.28	-0.17	-0.11	+0.01	+0.16	+0.01	-0.17	±0	+0.12	-0.18	+0.06
December .	-0.53	+0.84	-0.22	-0.08	-0.41	+0.56	-0.19	+0.04	-0.12	+0.27	-0.03	-0.12
January . .	-0.46	+0.38	-0.02	+0.10	-0.12	+0.13	-0.07	+0.07	-0.34	+0.25	+0.04	+0.03
February .	-0.42	+0.20	-0.21	+0.42	-0.11	+0.15	-0.26	+0.21	-0.31	+0.05	+0.05	+0.21

It is recognised of course that "normal" is the mean of the four years and is not necessarily the average conditions for the district for the long period, but it is necessary to use this value for the meteorological conditions as I have only these four years from which to calculate the trap departures.

The population throughout the winter of 1934 to 1935 and the summer of 1935 remained above normal but after that the changes are irregular.

Forecasting.

If the above reasoning is correct, there is for 48 consecutive months a measure of the log. (or percentage) departures of the population from the normal, as given in the last four columns of Table 47; also there is a strong indication that rainfall is an important factor in determining this, although it was found to be of little importance in determining activity.

I can now apply the same statistical process of partial regressions, to find out how far these population changes can be accounted for by changes in the weather conditions in the period preceding the catch.

This has been done for the effect of the two factors minimum temperature and rainfall, for each of the three preceding months on the population departure for each month. The data for this are given in Tables 47 and 48. Thus, for example, the population departure for July 1933 is -0.24 (Table 47). The minimum temperatures in the three previous months of June, May and April were -0.6, +2.0 and +1.1, and the rainfall departures -1.90, +0.36 and -0.89 respectively (Table 48).

A preliminary calculation showed that there was considerable difference of effect between the winter and summer, so that finally separate calculations were made for the six "winter" months, November to April, and the six "summer" months, May to October. It would have undoubtedly been better if regressions could have been taken for shorter periods still, but even 24 months is a small number of repetitions on which to get anything like a reliable estimate of the effect of six "independent variables."

The resulting regressions for winter and summer are shown in Table 49. It will be seen that in the winter months the changes in population are best explained on the assumption that 1° F. change in the mean minimum temperature of the previous month is associated with a change of 0.0456 in the log. of the "population." A similar change in the mean minimum temperature of two months previous produces an effect of only one-third of this, while in three

TABLE 48.

Departures of minimum temperature and wind from the normal in the 48 trap months and predictions of the catch departure (and hence the population) calculated from these data.

	Departure of minimum temperature from mean of same month in 4 years				Departure of rainfall from mean of same month in 4 years (in inches)				Dept. of population predicted from regressions on minimum temperature and rainfall in 3 months previous to catch			
	1933	1934	1935	1936	1933	1934	1935	1936	1933	1934	1935	1936
Winter :												
March . . .	+0.1	-2.5	±0	+2.2	+0.98	+0.63	-1.16	-0.46	-0.15	-0.16	+0.09	-0.11
April . . .	+1.1	+0.2	+0.6	-2.0	-0.89	-0.40	+1.82	-0.53	+0.04	-0.15	-0.02	+0.08
Summer :												
May . . .	+2.0	-0.4	-2.0	+0.2	+0.36	-0.30	+0.62	-0.69	-0.04	-0.14	+0.12	-0.10
June . . .	-0.6	-0.5	+0.8	+0.4	-1.90	-1.23	-0.08	+3.20	+0.04	-0.05	+0.22	-0.13
July . . .	+1.5	-0.5	-0.4	-0.8	-0.63	-0.91	-1.06	+2.60	-0.17	-0.16	+0.18	+0.15
August . .	+1.7	-1.5	±0	-0.2	-0.47	+0.74	+0.47	-0.74	-0.25	-0.23	-0.08	+0.56
September	+0.8	-0.8	-1.3	+1.4	-0.84	-0.46	+1.07	+0.22	-0.28	-0.09	-0.07	+0.45
October . .	+1.0	+1.5	-0.8	+1.7	-0.57	-0.02	+0.87	-0.27	-0.17	-0.13	+0.10	+0.08
Winter :												
November .	+0.6	+0.8	+1.0	+2.3	-1.63	-1.17	+2.09	+0.71	+0.01	+0.09	-0.05	-0.07
December .	-5.2	+7.3	-1.9	±0	-2.11	+2.28	+0.30	-0.47	-0.01	+0.05	+0.09	-0.14
January . .	-2.0	+1.4	-0.5	+1.1	-0.79	-1.90	+1.14	+1.55	-0.29	+0.34	-0.06	-0.02
February .	-3.0	+3.0	-3.0	+3.1	-1.80	+0.41	-0.12	+1.51	-0.23	+0.14	-0.01	+0.10
Minimum temperature departure					Dec. 1932		Jan. 1933		Feb. 1933			
Rainfall departure					+0.15		-0.38		-0.4			
					-1.96		-0.89		-0.44			

months previous it produces a negative effect (not significant). Rainfall, on the other hand, produces only much smaller effects varying from 0.007 to 0.019 per inch per month, the more distant month having the larger effect.

It must be noted that the variation in minimum temperature departure, from +7.3 to -5.2, during the 24 winter months is nearly three times as great as the variation in rainfall, from +2.28 to -2.11. So that the total effect of temperature is very much greater than that of rainfall.

TABLE 49.

Partial regressions of log. catch departure (after correction for activity) on the minimum temperature and the rainfall in the three previous months.

	24 Winter months		24 Summer months	
	6 factors	3 factors	6 factors	3 factors
Minimum temperature—				
month previous .	+0.0456	+0.0508 ± 0.0101	-0.0237	—
month two previous . .	+0.0151	+0.0135 ± 0.0097	-0.0003	—
month three previous . .	-0.0138	-0.0130 ± 0.0105	+0.0135	—
Rainfall—				
month previous .	+0.0101	—	+0.0916	+0.0910 ± 0.0234
month two previous . .	+0.0071	—	+0.1079	+0.1156 ± 0.0231
month three previous . .	+0.0194	—	+0.0696	+0.0645 ± 0.0224

In the summer months the values are very different. In fact the regression on temperatures is apparently negative (but not significantly so) for both previous and pre-previous months, but small and positive for three months previous. The rainfall, on the other hand, is of major importance and all three rainfall regressions are high. In addition to this it should be noted that

the variability of the rainfall in summer remains high, while that of temperature is much smaller than in winter. In the 48 summer months the minimum temperature departure only varied from $+ 2.0$ to $- 2.0$ degrees; while the rainfall varies from $+ 3.20$ to $- 1.90$: a greater range than the temperatures.

Thus it appears that in the winter the population changes are chiefly associated with temperature changes in the previous three months, while in the summer the effect of temperature is almost negligible but there is a high positive relation with rainfall.

This result is a natural one, as in the Harpenden climate rainfall is evenly distributed throughout the year, but there are large changes of minimum temperature. In the summer the temperature is high for the amount of rainfall, while in the winter it is low. Thus it is reasonable that the rainfall should be the limiting factor in the summer and the temperature in the winter.

From these regressions and the known departures of temperature and rainfall an estimate can be made of the population departures for each month. This has been done and the values indicated in the last four columns of Table 48, and also diagrammatically by the dotted lines in fig. 24.

Thus there are in fig. 24 two measures of the population: (1) the solid line which is calculated from the trap catch by correcting this for activity caused by weather conditions during the particular month (Table 47 last four columns); and (2) the dotted line which is calculated from the weather conditions of the three previous months (Table 48 last four columns) and does not bring in either the trap catch or the weather of the current month. It will be seen that on the whole there is a very close resemblance between the two.

If a longer series of results had been available separate regressions could have been calculated for shorter periods—say, spring, summer, autumn and winter, and a still closer agreement might have been expected.

With the two calculations, one for summer and one for winter, and the six partial regressions analysis of variance is as follows:—

	Degrees of freedom	Total variance	Mean variance
Summer :			
Total	23	1.3382	0.0583
	6	1.0241	
Residual	17	0.3141	0.0185 = 32%
Winter :			
Total	23	0.6498	0.0283
	6	0.4212	
Residual	17	0.2286	0.0134 = 47%

Thus for the winter months 53% of the mean variance is explained by the six factors and in the summer months 68%.

As it appears that a very small amount of variance is accounted for in winter by rainfall and in summer by temperature a second set of regressions were calculated on the rainfall in the three previous months for the summer and the temperature in the three previous months in the winter. These are shown in Table 49. They differ only slightly from the previous regressions.

The analysis of variance for these three factors only is as follows:—

	Degrees of freedom	Total variance	Mean variance
Summer :			
Total	23	1.3382	0.0583
	3	0.9765	
Residual	20	0.3617	0.0181 = 31%
Winter :			
Total	23	0.6498	0.0283
	3	0.4008	
Residual	20	0.2490	0.0125 = 49%

Thus the residual mean variance is actually slightly smaller in both summer and winter when only three factors are used.

FUTURE WORK.

The results described above have been based on four years continuous trapping of insects with a single light trap, at Harpenden about 25 miles north of London. Nearly all the calculations have been made with the total catch of all insects.

If conditions permit of the experiments being continued and extended the following suggestions are made.

1. The results should be applied as soon as possible to smaller groups and particularly to individual species, and perhaps even to separate sexes of one insect. To do this with satisfactory results the number of insects caught must be greatly increased.

2. The work, whenever it is done, should be carried out with at least four traps working simultaneously under as far as possible similar conditions. This will give larger numbers of a single species and reduce the sampling error.

3. It is most important that the work should some day be repeated in a different locality, and preferably in a different climate. A series of trap catches from a tropical climate, when temperature is not the most important factor, would be of particular interest.

4. Any species of insect chosen for investigation should have the following characteristics :—

- a. It should be readily attracted to light;
- b. It should be abundant at times;
- c. It should have a very long brood or a series of broods during the year;
- d. It should be very easily distinguished from any other insect liable to be caught in the trap;
- e. If possible the sexes should be easily distinguishable.

Among insects with which I have had personal experience the Trinidad Sugar Cane Froghopper (*Tomaspis saccharina*) appears to be a very suitable insect as it has 2 to 4 broods a year and the males come to light in very large numbers.

In this country analysis is already proceeding on about half a dozen species of moths which came to the present trap in large numbers, but the general result is to indicate that unless at least 1000 individuals are caught in a single brood the error is far too large to give any reliable results.

ACKNOWLEDGEMENTS.

Full acknowledgements have already been made in Part I of this paper and no additional names need be mentioned here. Perhaps, however, it would be as well to state that although I have received very great help and encouragement from the statistical department at Rothamsted, they are not responsible for the general argument or for any mistakes that may appear therein. I must take full responsibility for these and for the fact that I have used in analysis some less orthodox methods of demonstration because I believed them to be easier for the general entomologist to understand.

SUMMARY.

The analysis is based on four years captures in a light trap at Rothamsted Experimental Station. The trap was working on 1407 nights between March 1933 and February 1937 and caught altogether about 850,000 insects.

An account is given of the normal weather conditions in the district and also of the weather during the four trap years.

The sources of error were reduced as far as possible, and it was found necessary to deal with changes in the catch in geometrical or logarithmic proportion.

The catch is dependent chiefly on the two factors of activity and population, and, of course, only measures the positively phototropic nocturnal insects.

The analysis of the individual effect of each weather factor is made more difficult by the close correlation which exists between many of the weather factors themselves.

The first analysis was a simple comparison of the weather conditions on nights of high and low catch. On the good nights the minimum and the grass minimum temperatures of that night and the maximum temperatures of the previous day were all higher than on the poor nights; the wind was also calmer; the moon closer to new moon than to full, and the barometer high. Rain during the previous daytime is associated with low catch, but rain during the night occurs with equal frequency with high as with low catch. Relative humidity also appears to be more or less similar in both series.

A short account is then given of the statistical method of regressions and it is shown that activity is most likely to be correctly estimated by using as a basis of calculation the difference between successive days in both catch and weather conditions. The effect of minimum temperatures, considered alone, is that a change of 1° F. is associated with a change of log. catch of about 0.060, or, in other words, the catch is doubled by an increase in minimum temperature of 5° F. (or just under 3° C.). There is no evidence from the data available that this figure alters with the season, the differences found from month to month are irregular and not outside the limits of non-significant variation. Results for Lepidoptera only and Hemiptera only give values which do not differ significantly from the value for total insects.

The effect of maximum temperature alone is smaller than that of minimum temperature and the average effect (over the 4 years) is that 1° F. change is associated with 0.042 change in log. catch, or the catch is doubled with a rise of about 7° F.

The grass minimum alone (calculated from 6 months results) shows a regression of 0.030. The regression on daily range of temperature (from 3 months) is only—0.004, which has no significance.

Relative humidity at 9 p.m. shows a small but probably significant regression of about 0.008 change in catch produced by 1% change in humidity.

Insects fly later on cloudy nights, probably owing to the slow fall in temperature. The effect of fog is uncertain; usually it occurs on cold nights with very poor catch, but one very foggy night in September 1933 gave high catches in the family NOCTUIDAE.

The catch is lower at full moon than at new moon and there are asymmetries in the effect that can be explained by similar asymmetries in the times of rising and setting of the moon.

Wind force was divided into six artificial groups, the lowest being dead calm and the highest wind over 20 m.p.h. The effect is complicated by the

fact that the windy nights are warmer than the still nights, particularly in the winter. When the method of difference between successive days is used the effect of a change of one group was to alter the log. catch by 0.095 (other factors being neglected).

The effect of barometric pressure is complicated and difficult to understand. Catch is low with low barometer, and high with high barometer unless pressure is falling; in this latter case the catch is distinctly lower. If the direction of movement is neglected the average effect of a rise of 1 in. in the barometer is to add 0.668 to the log. catch. The catch is therefore doubled by a rise of 0.48 inches (= 1.14 cms.).

There is no evidence of the effect of thunderstorms on the total catch of all insects, but slight indication that moths of the family NOCTUIDAE are more abundant during thundery weather.

The simultaneous analysis of several factors acting together show differences from some of the above results owing to correlation between the weather conditions themselves. Analysis of 9 p.m. temperature and humidity, expressed as Relative Humidity, Absolute Humidity and Saturation Deficiency, shows no advantage to be gained by using one method rather than another.

With partial regressions of catch on the minimum temperature of several nights preceding the catch, it was found that the previous night has about $\frac{1}{5}$ of the effect of the current night, but the night before that had on an average no effect.

When maximum and minimum temperatures and wind were taken simultaneously the regressions of each were 0.023; 0.070 and 0.144 respectively.

For the year 1933 the simultaneous effect of the above three factors plus 9 p.m. relative humidity was calculated and the regressions were 0.016; 0.065; 0.121 and 0.006.

It is possible to correct the mean catch for each month for the effect of its departures from the normal in temperatures, wind, etc., thus getting a value for what the catch would have been if all conditions had been normal for the month. The differences then remaining are due to population effects. These values have been calculated for the 48 months in which the trap was running.

The relation of these values to the rainfall and minimum temperature of the three previous months has been calculated and two regression formulae obtained, one for winter and one for summer, from which the population changes can be estimated from a knowledge of previous weather conditions only. Rainfall is most important in summer and temperature in winter.

The population changes as estimated from the trap catch and as calculated from the rainfall and temperature in the three previous months are shown in fig. 24, and it will be seen that they are closely similar. Between 50% and 60% of the variance of the population has been accounted for.

Thus a beginning has been made in the problem of measuring the variations in abundance of insects and in forecasting this from a knowledge of the weather conditions. So far it has only been described for the total population of all insects but it will later be extended to single species.

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